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The perception of illusory contours in young and older observers

An explorative study using psychophysics and EEG

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Zusammenfassung

In dieser Arbeit wird eine Reihe von psychophysischen und EEG-Experimenten vorgestellt, die den Einfluss normaler Hirnalterungsprozesse auf die Wahrnehmung von Scheinkonturen (SKen) erfassen sollen. SKen stehen hier als stellvertretendes Paradigma für visuelle Bindungsprozesse („visual binding“), die für viele komplexe visuelle Situationen, wie etwa Auto fahren, notwendig sind. SKen werden zudem häufig im Kontext von klinischen neuropsychologischen Untersuchungen angewendet. Nachdem die Wahrnehmung von SKen bis dato noch nicht systematisch in älteren Bevölkerungsschichten untersucht worden ist, könnten unsere Ergebnisse auch hierfür eine Grundlage bieten.

Insgesamt nahmen 153 gesunde Probanden zwischen 18 und 90 Jahren an zwei psychophysischen und zwei EEG-Experimenten teil. In unserem ersten, explorativen, Verhaltensexperiment stellten wir fest, dass die Zeit für die Erkennung von SKen (im Vergleich zu Kontrollreizen) stetig mit dem Alter anstieg, was ein graduelles Nachlassen der visuellen Bindungsfähigkeiten mit zunehmendem Alter nahe legt – ein Prozess, der bereits im Alter von 30 Jahren einsetzt. Dieser Effekt konnte nicht allein durch die wohl dokumentierten Schwierigkeiten älterer Menschen bei der Verarbeitung von Reizen, die exzentrischer im Gesichtsfeld liegen (z.B. Poggel & Strasburger 2004; Sekuler et al. 2000; Kosslyn et al. 1999) erklärt werden, da wir zu den gleichen Ergebnissen gelangten, als wir die Reizgröße in einem zweiten Experiment von 10 auf 5 Sehwinkelgrad verkleinerten.

In unserem ersten EEG-Experiment, einem passiven Paradigma, konnten wir weder bei unseren jungen noch älteren Probanden einen sogenannten SK-Effekt replizieren, also eine differentielle Reaktion zwischen SK- und Kontrollreizen, die als physiologisches Korrelat der Gestaltwahrnehmung angesehen wird (z.B. Murray et al. 2004, 2002; Kruggel et al. 2001; Herrmann & Bosch 2001). In unserem zweiten EEG-Experiment reduzierten wir die Reizgröße von 6 auf 4 Sehwinkelgrad, was jedoch nur einen schwachen Anstieg differentieller Aktivität bei den jungen Probanden zur Folge hatte. Erst als wir im zweiten Teil des Experiments durch eine Änderung der Instruktion und die Einführung von Zielreizen ein bewusstes Verarbeiten der dargestellten Reize erzwangen, fanden wir in beiden Gruppen einen deutlichen SK-Effekt, was nahe legt, dass die SKen in diesem Falle wahrgenommen wurden. Dieses Ergebnis untermauert die Bedeutung sogenannter „top-down“ Faktoren bei der SK-Wahrnehmung – ein Thema, welches nach wie vor kontrovers diskutiert wird (z.B. Senkowski et al. 2005; Vuilleumier & Landis 1998; Davis & Driver 1994; Pritchard & Warm 1983). Insgesamt sprechen unsere Ergebnisse dafür, dass die Wahrnehmung von SKen zwar im Alter abgeschwächt oder verlangsamt wird, dass dieses Defizit jedoch von kognitiven Strategien kompensiert werden kann.

Abstract

A series of psychophysical and electrophysiological (EEG) experiments are presented which aimed at assessing the effect of normal brain aging on the perception of illusory contours (ICs). ICs were here considered as exemplary tasks for the process of visual binding, as required for the handling of complex visual situations such as car driving for example. Furthermore, ICs are often used in the context of clinical neuropsychological assessments. Since as yet IC perception has not been systematically studied in the elderly population, our data can provide a baseline measure.

A total of 153 healthy paid volunteers, aged between 18 and 90 years, took part in two psychophysical and two electrophysiological experiments. In our first explorative behavioural paradigm we found that the time to identify ICs of the Kanizsa type (compared to control stimuli) increased steadily with advancing age, suggesting a gradual decline in visual binding capacities, which starts already from the age of 30 years on. The observed effect could not be explained by older people's well documented deficits in processing stimuli at higher eccentricities (see for example Poggel & Strasburger 2004; Sekuler et al. 2000; Kosslyn et al. 1999), since it proved robust, also when we reduced stimulus size from 10° to 5° of visual angle in our second psychophysical experiment.

In our first EEG experiment – a non-response paradigm – we did not replicate previous findings concerning an IC effect, i.e., a differential electrophysiological reaction between IC and control stimuli, which is considered to reflect the perception of the "Gestalt" (see for example Murray et al. 2004, 2002; Kruggel et al, 2001; Herrmann & Bosch 2001). The replication failed for both our young and older observers. A reduction of the stimulus size from 6° to 4° of visual angle in our second EEG experiment brought only a slight increase of differential activity in the young observers. Only when we induced a conscious processing of the presented shapes by introducing new target stimuli in the second part of this experiment, did we find a distinct IC effect in both subject groups, suggesting that the IC stimuli were perceived. This finding speaks for the importance of top-down influences in IC perception, an issue that still provokes considerable debate (Senkowski et al. 2005; Montaser-Kouhsari & Rajimehr 2004; Vuilleumier & Landis 1998; Gurnsey et al. 1996; Davis & Driver 1994; Pritchard & Warm 1983). Our findings suggest that the perception of ICs is weakened or delayed with advancing age, but that this deficit can be compensated for by cognitive strategies.

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1. Introduction

When our visual system is intact, we move through our environment with incredible ease. With a single glance we are able to get the gist of a visual scene (Thorpe, Fize and Marlot, 1996), which allowed our early ancestors to flee from approaching predators and helps us nowadays to step on the brakes in time when we see a child running onto the road.

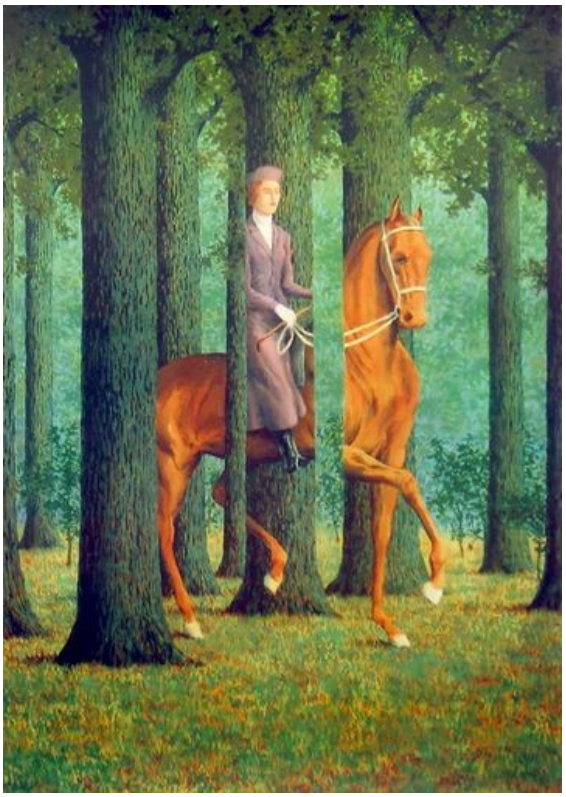

Figure 1: Le blanc-seing (René Magritte)

Figure 1 illustrates another capacity of our visual system: the capability to handle ambiguous or missing information. We recognize a woman riding a horse in a forest, even though the trees and gaps in between are arranged in a way that is not possible in reality, and parts of the horse and rider are missing from the retinal projection. The latter phenomenon – that objects are partially occluded by other objects – is, however, frequently encountered in our every day life. Yet we are still able to identify for example a car when some people are standing in front of it, excluding some parts from our view. All this indicates that “seeing” and visual perception are “more than meets the eye”, and rather are a complex and constructive process (see for example Ganis & Kosslyn 2007).

Most of the time we are unaware of the enormous computational work that lies behind the rapidity of visual perception. The only information available is light of varying spatial and spectral composition stimulating our retinal receptors, yet our visual system is able to reconstruct a complete three-dimensional representation of the outside world within milliseconds.

In order to arrive at this representation, many processing stages are implicated, which comprise the decomposition of the retinal image into its elementary components (such as colour or orientation; see for example Treisman & Souther, 1985), which are processed in specialized cortical areas and subsequently reintegrated to form a coherent image ("binding").

The segregation of visual sensory input into coherent objects requires, amongst others, the identification of borders between the various image components and surfaces. Normally, the borders of an object are defined by physical differences in luminance, texture, and / or chrominance. But contours can also be perceived in the absence of a real, physical discontinuity (Ginsburg, 1975; Petry & Meyer, 1987). A variety of names have been ascribed to contours that are perceived despite the absence of a luminance gradient, including "illusory contours", "subjective contours", "phenomenal contours", "cognitive contours", "anomalous contours", "quasiperceptive contours", "unfinished contours", "incomplete contours", "virtual contours", "contours without gradients", "apparent contours" (see for example Kanizsa, 1979; Petry & Meyer, 1987; Purghe´ & Coren 1992). "Illusory contours" (ICs) has emerged as the term which is most widely used in English and which will from now on be referred to in this dissertation.

Illusory contours can be induced by different stimulus configurations, such as abutted lines or gaps in gratings (see Figure 2), but figures of the Kanizsa type (see Figure 3) certainly represent the most popular example of ICs. Stimuli of that type are generated by a particular configuration of distant high-contrast borders, such as incomplete and co-aligned white (or black) circles ("pac-men") that induce the illusory perception of a dark (or light) shape, placed over the white (or black) circles (Kanizsa, 1979).

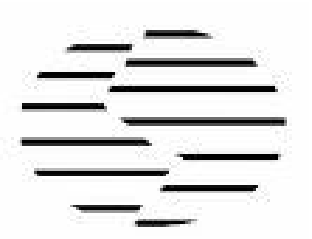

Fig. 2: Abutting line grating

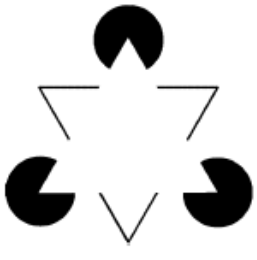

Fig. 3: Kanizsa triangle

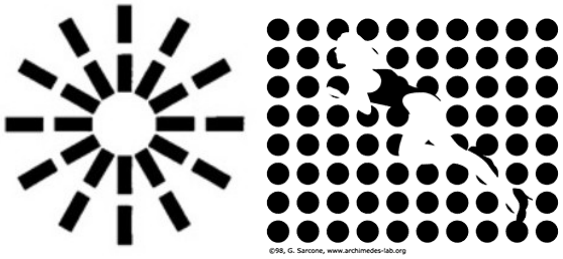

Fig. 4: other examples for illusory contours

Looking at Figure 3, we almost instantly perceive a white triangle which is superimposed on three black discs. This impression arises very naturally and effortlessly and persists even if we are aware that that shape is not “real” (Ware & Kennedy, 1978). According to Kanizsa (1976; see also Prazdny 1986), this special illusion comprises three perceptual aspects: 1. the impression of a surface superimposed on the inducing elements (stratification); 2. the luminance of the superimposed object seems to be brighter than the background; 3. the perception of illusory (physically non existent) contours that outline the object.

Kanizsa figures have been the subject of many studies in the recent years, as they offer a possibility to gain insight in perceptual grouping and segmentation mechanisms (see for example Marr, 1982), and in general, an understanding of the constructive aspects of human vision.

The following chapters will comprise an overview on the current state of research on illusory contours. The first two chapters describe research findings from animals and humans, aiming to identify the brain structures and processes implied in the perception of ICs. IC perception is known to vary with certain factors; the third chapter will discuss a selection of stimulus-, subject- and other factors, which are most relevant to this thesis. Among these factors, the effect of advanced age on IC perception has as yet not been investigated. Yet, possible deficits in completion processes (such as required for the perception of ICs) might have an impact on daily living activities of older individuals, for example car driving. The final chapter of this introduction will describe anatomical and morphological chances of the aging visual system and results of behavioural experiments with older observers which are related to our central question.

1.1. Neural bases of IC processing

A large part of research on illusory contours concerns the question on which cortical level they are encoded.

1.1.1. Single unit neurophysiology

In a groundbreaking experiment, von der Heydt et al. (1984) were the first to provide direct evidence that early visual areas are involved in representing ICs. Using intracellular recording, they found that a moving illusory bar could excite V2 neurons in monkeys even when there was no stimulus in the neuron’s receptive field.

In further studies, von der Heydt and Peterhans (1989) found that 44% of V2 neurons in monkeys were signalling the orientation of ICs (defined by abutting gratings), and 32% of V2

neurons were responding to illusory bars of Kanizsa-type figures (Peterhans and von der Heydt, 1989).

Other intracranial animal studies, using abutting line gratings or Kanizsa-type figures as stimuli, equally reported effects in V2 (Leventhal et al., 1998; Nieder and Wagner 1999; Bakin et al., 2000) and sometimes also in area V1 (in cats: Redies et al., 1986; Sheth et al., 1996; Lee and Nguyen 2001; Ramsden et al., 2001). Only the early visual areas contain neurons with small receptive fields for encoding information with high spatial precision and feature resolution and therefore seem suited for representing the perceived sharp contours explicitly.

In a single-unit recording with optical imaging in monkeys, Ramsden et al. (2001) found that both V1 and V2 neurons responded to ICs defined by abutting gratings, but that their orientation was negatively signalled in V1 as compared to real contours. They proposed that this de-emphasis of IC-orientation in V1 in combination with the normal positive IC responses in V2 could provide a unique signature for the neural representation of ICs in comparison to real contours.

Although all these data support the idea that early visual areas play an essential role in IC processing, they do not exclude the possibility that the observed activation could also be the result of a feedback process from higher visual areas. Studying the temporal evolution of neuronal activities in response to a static display of Kanizsa figures (in rhesus monkeys), Lee & Nguyen (2001) found that the response to illusory contours emerged in V1 at about 100 ms, which was significantly later than the emergence of the illusory contour response in V2. Furthermore, the V2 response was stronger than the one observed in V1. The authors interpreted their observation in a sense that the completion of the ICs in V1 could be effectuated by a feedback modulation from V2.

Taken together, results from single unit neurophysiology provide evidence for the importance of lower visual areas in IC processing. Most authors agree, however, that IC processing is not a simple bottom-up feed forward process, but rather an interactive process involving complex inter-cortical interactions between early visual areas.

1.1.2. Electrophysiology in humans

On the electro-physiological level, numerous studies have tried to characterize the so-called IC effect, i.e. the differential reaction between an IC and a non-shape (NS). Concerning visual evoked potential (VEP) wave-form analyses, most authors report a first differential reaction in occipital regions, occurring around the N150 (Kruggel et al, 2001; Herrmann &

Bosch 2001; Murray et al. 2004, 2002; Halgren et al. 2003; Korshunova 1999). This component is thought to reflect the perception of the « Gestalt » (Kruggel et al. 2001; Herrmann & Bosch 2001). Comparing IC to real contour stimuli (RCs), the peak of the N150 was reported to arrive later for ICs than RCs, but with higher amplitude (Pegna et al. 2002). The global field power (GFP) is higher for ICs than for RCs or NSs (Murray et al. 2004; Pegna et al. 2002).

Although the spatial resolution of EEG does not allow pinpointing the locus of activation with the same accuracy as for example fMRI or PET, results from a number of investigations put forward that the IC effect is most pronounced in lateral / occipital regions of the cortex (Murray et al. 2004; Halgren et al. 2003; Korshunova 1999; Proverbio & Zani 2002).

Another question often raised in this context concerns lateralization; the right hemisphere is supposed to promote a global view of an object, whereas the left hemisphere has been associated with the perception of elements in detail. Results from studies investigating this aspect are, however, inconsistent. Using an EEG paradigm, Proverbio & Zani (2002) found that the amplitude of the N150 was higher in the right hemisphere than in the left hemisphere, which was however not specific to the IC condition but concerned RCs and NSs likewise. Murray et al. (2002) have also studied this question by presenting stimuli to one hemifield only; they found no evidence for an interaction of the absence/presence of an IC with the hemisphere. Halgren et al. (2003), using MEG methods, reported more right hemisphere activity in the IC condition. Brighina and collaborators (2003) applied transcranial magnetic stimulation (transitory inhibition of activity in the stimulated areas) for studying the areas involved in IC perception. In a reaction-time task they found a significant increase of reaction times for ICs following right occipital stimulation.

1.1.3. Functional imaging

Results from functional imaging (PET / SPECT / fMRI) concerning the locus of IC processing are rather ambiguous, although a certain degree of variation can surely be explained by the variety of different approaches that have been applied (see Seghier and Vuilleumier 2006 for a review).

The first study using fMRI techniques by Hirsch et al. (1995) reported activation related to flickered Kanizsa stimuli only in extrastriate visual areas (in particular V2), predominantly in the right hemisphere, therefore contradicting the results from single unit neurophysiology to a certain degree. The authors concluded that IC perception may be accomplished outside area V1 (Hirsch et al. 1996); yet, the activation they had observed was near the cortical region

onto which the vertical meridian projects between V1 and V2, so a possible involvement of V1 should not be entirely ruled out (Hirsch et al. 1995).

By contrast, Larsson at al. (1999), using static abutted lines in a PET study, found a strong bilateral activation in V1 and V2 which was, however, not specific to IC but was also observed during the perception of real contours. They furthermore reported activation of the fusiform and lingual gyri, the cuneus, and the parietal lobe. However, according to their data, the right fusiform gyrus was the only region specifically activated by ICs.

Further studies produced a variety of results, only partially confirming activity in lower level visual areas V1 and V2 during IC processing: Fftyche and Zeki (1996) reported no activation of V1 but a robust bilateral activation of V2 and a possible implication of V3 in a PET study. Goebel et al. (1998) equally found no significant V1 activity in an fMRI study on apparent motion of IC, but an implication of V2 and V5. In an fMRI experiment, Mendola et al. (1999) found only feeble V1 and V2 activity after individual analysis, but reported strong activation in the Lateral Occipital Complex (LOC), including V3A, V4v, V7 and V8. Seghier et al. (2002) presented moving ICs in an fMRI experiment and reported activation in V1 and V2, as well as in V5, the Lateral Occipital Sulcus as well as the Kinetic Occipital.

Several authors could not evidence activation of V1 and V2 during IC perception: In a combined EEG / fMRI experiment, Kruggel et al. (2001) reported IC-related activity in different parts of the lateral occipital gyrus, including the V5a area. Murray et al. (2002) also found strong activation in the LOC, as well as the right parietal cortex. While several authors (Pegna et al., 2002; Murray et al., 2002, 2004; Stanley and Rubin 2003) reported a bilateral activation of the LOC, Ritzl et al. (2003) found stronger effects in the left hemisphere. Specific IC related activity was furthermore found in the right parietal region (Stanley and Rubin 2003) and the posterior parietal regions (Murray et al. 2004).

Summing up those findings, the role of V1 in IC processing has not been consistently supported by the results from functional imaging. A majority of results speak in favour of an involvement of V2. Fftyche and Zeki (1996) and Hirsch and al. (1995) even reported stronger activity during IC perception as compared to real contours. As mentioned above, however, many studies did not evidence significant IC related activity in low level visual areas.

The role of the Lateral Occipital Complex in IC perception has received more support from functional imaging. It has, however, been argued that this region is generally implicated in the recognition of coherent objects and bounded surfaces (Grill-Spector et al., 2003, Vuilleumier et al., 2002); and since illusory contours normally delimitate an illusory figure, observed activation in the LOC region may rather reflect the processing of the figure as an

object than the processing of an illusory contour per se (Kourtzi and Kanwisher 2001; Yin et al., 2002; cited by Seghier and Vuilleumier 2006).

The right fusiform gyrus has been proposed as another candidate region for IC perception. Larsson et al. (1999) reported higher activation of this area during the processing of ICs than during the processing of real contours and the right-hemispheric activation pattern in the study by Hirsch et al. (1995) was also likely to include the fusiform region.

Finally, an IC related activation of posterior parietal regions (Halgren et al., 2003; Murray et al., 2004), the lingual gyrus (Halgren et al., 2003) and the orbitofrontal cortex (Halgren et al., 2003) have been reported in some studies, but these results have not been consistently confirmed.

The issue of a possible hemispheric lateralization of IC processing is not resolved to the present. Functional imaging data sometimes speak in favour of a lateralization (for example Hirsch et al. 1995), sometimes not (for example Fftyche & Zeki 1996; Larsson et al. 1999; Mendola et al. 1999).

1.1.4. Clinical research

Relatively little research has been performed on IC perception in clinical populations. Huxlin et al. (2000) tested IC perception in monkeys with a lesion of the inferotemporal cortex and found that this impaired the monkey's ability to see illusory contours.

Vuilleumier & Landis (1998; see also Vuilleumier et al. 2001) investigated 64 - 74 year old patients, suffering from a left-sided hemineglect, with a figure bisection task (IC or RC). They found no decrease in performance when ICs were presented in the hemifield contralateral to the lesion.

The work of Grabowska and collaborators (2001) has contributed an interesting aspect to this issue of lateralization: they investigated the effects of hemisphere and gender in brain-lesioned individuals. In brain-lesioned women they did not find hemisphere effects although reaction times were generally slower than in the control group. In male subjects, however, individuals with right-sided lesions showed significantly impaired IC perception while results from individuals with left-sided lesions did not differ from the control group. It could be hypothesized, that IC perception was lateralized to the right hemisphere in men, but is not lateralized in women.

1.2. Processes implied in the perception of IC

The neural mechanisms of IC perception are still not completely understood, although a large body of research has been dedicated to this question. In an extensive review, Seghier and Vuilleumier (2006) recently attempted to integrate the findings from psychophysics, electrophysiology and functional imaging. They proposed two basic mechanisms to be critically involved in IC perception with distinct anatomical and temporal characteristics.

As a first mechanism they suggested a *"fast-local low-level mechanism"* that would predominantly be carried out by early visual areas V1 and V2. Studies from psychophysics (for example Dresp and Bonnet 1993; Pillow and Rubin 2002), neurophysiology (for example von der Heydt et al. 1984) and functional imaging (for example Hirsch et al. 1995, Larsson et al. 1999) have delivered of evidence for the implication of these areas in IC processing. Their organizational structure – with small receptive fields in retinotopic coordinates – would furthermore make them ideal tools for the detection of local details as edges and contours, which serve as basis of figure-boundary detection (Li, 2003). Haynes et al. (2004) also suggested that this local process might involve some initial representation of candidate surfaces of the illusory figure, based on relative-brightness and contrast information.

Concerning the timing of processes in low-level areas, Lee and Ngyuen (2001) contributed some interesting findings, based on single unit recording in monkeys: they observed a first neuronal response occurring in V2 at 65–95 ms, and slightly later, around 100–120 ms post-stimulus, a response in V1. These results have been interpreted in terms of a dynamic interaction with rapid feedback projections from V2 to V1 which enhance and sharpen visual processing at a relatively local scale (for example Roe et al., 2005). The features extracted by low level vision would then be forwarded to higher cortical areas for further processing (see for example Saarinen and Levi, 2001; Fujita et al. 1992).

According to Seghier and Vuilleumier (2006), the second mechanism, a *late-global high-level* process, would then bind the various stimulus features into a coherent percept. Supported by numerous findings from functional imaging, the LOC has emerged as the primary candidate for this process; LOC areas have been shown to be critically involved in the recognition of two- and three-dimensional shapes (see for example Grill-Spector et al. 2001), regardless of the visual cues defining the object's contours or surface. The LOC, like other higher-tier cortical visual regions that have been suggested to play a role in IC perception (such as the fusiform gyrus or parts of the right parietal lobe; see previous chapter), is characterized by having large neuronal receptive fields which allow a representation of the global shape of a figure and "bridge the gaps" which are characteristic for Kanizsa type stimuli.

In order to reconstruct a coherent image from the elements extracted by low-level vision, a binding process is required. On the physiological level, it has been proposed that feature binding could be achieved by a synchronization of neuronal firing, oscillatory processes in the frequency range of around 40 Hz (gamma frequency) (Başar-Eroglu et al. 1996 ; Gray et al. 1989, Tallon et al. 1995).

Using magneto-encephalographic (MEG) methods, Tallon and collaborators (1995; Tallon-Baudry et al. 1996, 1997) investigated the electrophysiological reactions produced by IC perception. Presenting IC figures (illusory squares), non-shapes, and a target stimulus (a curved illusory triangle), the researchers observed a first burst of gamma activity, occurring at around 100 ms post-stimulus which was independent of the stimulus type; maximal gamma activity was measured at the vertex (Cz), around 210–290 ms. This second burst was varying with the presence/absence of IC, therefore the authors concluded that this element was associated with feature binding. Similar results have been reported by Herrmann and collaborators (Herrmann et al. 1999, Herrmann and Mecklinger 2000), who equally observed a first burst of gamma activity around 100 ms post-stimulus (which differed significantly between target and non-target) and a late differential reaction between IC and NS.

Once the binding of local stimulus features would be completed, the shape information would then be sent back to the early areas V1 and V2 to “work out the details”, e.g., strengthen the figure-ground segregation process and reconstruct missing contours (Vuilleumier and Seghier, 2006).

1.3. Factors that influence IC perception

A number of stimulus and subject parameters have been reported to modulate IC perception. An extensive overview – especially of stimulus parameters – can be found in Petry & Meyer’s book “The Perception of Illusory Contours” (1987). The parameters most relevant to this thesis are discussed below.

1.3.1 Stimulus parameters

Luminance contrast between inducers and background is a requirement for the Kanizsa illusion to occur. The illusion will not take place at equiluminance of inducers and background despite actual differences in colour or texture (Pradzny 1986; Cavanagh 1987; Li & Guo, 1995). ICs can be perceived if the inducers have opposite polarity (i.e., black / white inducers on white background); the perceived brightness of the illusory form has been found to vary with inducer polarity (Spehar et al. 2000), however. Furthermore, the perceived sharpness /

clarity of the illusory figure declines as the luminance of the visual field is reduced (Warm et al. in Petry & Meyer 1987).

One of the major factors modulating the perception of ICs is the so-called support-ratio (Kojo et al. 1993, Liinasuo et al. 1997): the perception of the IC is facilitated when the proportion between the side-length of the illusory form and the diameter of the inducing disks is small, i.e. a small illusory form with comparably big inducers. With a constant support ratio, the distance between inducers can be extended up to 13 deg of visual angle without a decrease in performance (Ringach & Shapley, 1996). Therefore, the support ratio constitutes a more important factor in IC perception than the actual distance (as visual angle) between inducers.

The perception of IC is furthermore bound to temporal constraints: to develop the perception of an IC, the minimal presentation time must comprise around 50-80 ms (Kojo et al. 1993; Mather, 1988). An IC can even be perceived when the inducers are presented sequentially, as long as the time interval between successive frames does not exceed 500 ms (Kojo et al. 1993).

Finally, the position of the IC in the visual field and fixation play a role. If an IC is gazed at directly, it will disappear. There is some debate about the question whether or not illusory figures pop out in visual search displays (see Chapter 1.3.3), but in general centrally presented IC are more easily perceived than laterally presented ones (Murray et al. 2002).

1.3.2. Subject parameters

Concerning age effects in the perception of ICs, a number of studies have aimed to assess from which age on infants perceive ICs. Most of these studies demonstrated that infants respond to ICs at the age of about 4 months (see for example Ghim, 1990; Otsuka et al., 2004; Kavšek 2009). Up until today, however, no systematic research has been conducted on age effects in adulthood and older age.

There are no known gender differences in the ability to perceive ICs, nor has this issue been addressed explicitly in any publication. Grabowska and collaborators (2001) have, however, contributed an interesting aspect to this question: investigating the effects of hemisphere and gender in unilaterally brain-lesioned individuals they found slower reaction times (compared to a control group), but no hemisphere effects, in brain-lesioned women. In male subjects, in contrast, individuals with right-sided lesions showed significantly impaired IC perception while results from individuals with left-sided lesions did not differ from the control group. They concluded that IC perception might be lateralized to the right hemisphere in men, but localized in both hemispheres in women.

Concerning clinical aspects, not many studies have been conducted on IC perception. As mentioned above, Grabowska and collaborators (2001) found diminished IC perception following brain lesions, but effects depended on the position of the lesion and patient gender. Vuilleumier & Landis (1998) investigated subjects suffering from a left-sided hemineglect (between 64 and 74 years) with a figure bisection task (IC or RC). Finding no performance decrease in the IC condition, they concluded that IC perception was a pre-attentive (bottom-up) process. In clinical routine, a behavioural test of the Kanizsa illusion is often administered to individuals susceptible of suffering from a dementia for testing gnosias. Visual agnosia often appears in the clinical profile of Alzheimer's disease. In fact, these patients often fail to perceive the illusion, but at present no systematic study on IC perception has been conducted in this population yet.

1.3.3. Top-down influences

One of the most elementary questions raised in the issue of IC perception is, whether it is a pre-attentive, automatic (bottom-up) process or whether so-called top-down processes (such as knowledge, memory or attention) play a major role. This question has provoked considerable scientific discussion and as yet no satisfying answer has emerged from the numerous investigations.

Attention is the top-down process that has received the widest interest in this debate: is attention necessary to achieve visual binding underlying the Kanizsa illusion? Frequently used approaches to test influences of attention in visual perception are based on visual search paradigms. According to the feature integration theory (e.g., Treisman & Gelade 1980), the search for information in a visual environment takes place in two steps: in the first, feature extraction stage, the different elements are coded in parallel across the whole visual field. In the subsequent feature integration stage, the single elements are recombined into objects by sequentially focusing attention to different parts of the visual field. If a target stimulus can rapidly be detected, without any influence of the number of surrounding distractor elements, a pre-attentive (bottom-up) process, which does not require directed attention, can be assumed to underlie. A serial search, revealed by a prolongation of response times as a function of the number of distractor items, suggests the involvement of attentional top-down processes.

Results concerning IC perception in visual search tasks have been ambiguous, though; Davis and Driver (1994) reported a « pop-out » of ICs in a visual search task, signifying that ICs could be detected in parallel (see also Gurnsey et al. 1992). Montaser-Kouhsari and Rajimehr (2004) comment on these results, that a parallel detection process would not necessarily indicate a non-attentive treatment. Other authors also reported opposite results (serial processing, therefore attentive search) in this task (Grabowecky & Treisman 1989; Gurnsey et al. 1996). A more recent study by Senkowski and collaborators (2005) yet again

spoke in favour of a pre-attentive process. In a combined psychophysical and EEG investigation they reported a pop-out of illusory figures in a visual search paradigm.

Visual search paradigms can, however, not answer the question whether spatial or object-based attention is necessary for IC perception, since obviously object-based attention is directed to the search target. But does the brain "bother" to build out ICs when we do not attend the concerning area of the visual field? This question is hard to answer, because we will never know whether we had "seen" the ICs, if we do not pay attention. In our every day life we are rarely confronted with configurations of the visual scene that are as salient as for example the Kanizsa illusion, so that we would notice them "popping out".

An approach to the issue of object-based attention was taken by Senkowski and collaborators (2005). In one of their experiments they used the surface of an illusory triangle as a cueing area for the appearance of a target on two possible locations. They indeed found a cueing effect – suggesting that the IC formation was completed in the absence of object-based attention. The authors commented, however, that this experiment comprised only two possible locations for target appearance, which might have directed more attentional monitoring to these areas. This attentional monitoring might, again, have made the Kanizsa figures more salient, underlining the role of attention in IC processing. Other researchers, who equally used cueing-paradigms (Martínez et al. 2007, Moore et al. 1998), support the view that boundary completion is performed pre-attentively, but that the perception of an illusory object is enhanced by spatial attention.

Another approach for estimating attentional influences on IC perception has been taken by Pritchard and Warm (1983) in a double-task experiment: subjects were performing a primary task which consisted of matching (same/different) IC or RC shapes. In half of the cases they had to simultaneously perform a secondary task charging working memory. In conditions with a secondary task, the increase of reaction times for ICs was significantly higher than for RCs, implying that attentional resources are required for IC processing.

The clinical data of Vuilleumier and Landis (1998) on hemineglect patients who successfully bisected illusory figures (see Chapter 1.3.2) suggest yet again that attention is no requirement for IC processing. Furthermore the fact that already very young infants (see previous chapter) and even insects and many other species (see Nieder 2002 for a review) respond to ICs suggests that IC processing is not dependent on higher cognitive (top-down) influences.

On the other hand it does seem likely that top-down processes modulate IC processing. For example, Wallach & Slaughter (1988) investigated memory effects on IC perception by

presenting more complex illusory shapes than those normally used (squares, triangles, etc.); the authors found that IC perception was facilitated if the shape had been shown before.

To sum up these results, the role of top-down mechanisms in the perception of ICs remains unclear. Many research results suggest that the neural mechanisms for IC construction can operate without the explicit allocation of attention or other top-down processes, which is also supported by computational models (see for example Grossberg & Mingolla 1987, 1985). Top-down processes nevertheless seem to have some modulatory influence. Altogether it seems that contour interpolation – as the first step of IC processing – happens pre-attentively, and that the subjective percept is subsequently enhanced or sharpened by top-down mechanisms.

1.4. Aging and the visual system

1.4.1. Anatomical and morphological changes

It is a well-known fact that aging affects the optics of the eye. Some typical age-related changes are presbyopia (a loss of accomodative amplitude), senile miosis (a decrease in pupil size), increased lenticular density (in severe form called cataract), and lenticular yellowing (Spear, 1993; Weale, 1963).

Less is known about age-related changes that occur further along the visual pathway. On the retinal level, some studies reported a disorganization of the outer segments of both rods and cones (Marshall, 1978; Marshall et al., 1979), an accumulation of refractile bodies (Tucker, 1986) and refractile particles (Curcio et al. 1993), or lipofuscin (Iwasaki & Inomata, 1988) in the inner segments of cone receptors. Others researchers reported a displacement of some photoreceptor nuclei (Curcio & Drucker, 1993; Gartner & Henkind 1981, Lai et al., 1982). Curcio and collaborators (1993) proposed that up to 30% of the rods in the central visual field (28.5 deg) were lost until the age of 90. There exist, however, indications that this loss may be compensated by synaptic growth in the remaining rod terminals (Jansen & Sanyal, 1992; electron-microscopic study in mice), so that the same amount of photons could be captured as in young observers (Curcio et al., 1993). Retinal cones seem less susceptible to the effects of aging, at least in the central visual field (Curcio et al., 1993; Gao & Hollyfield, 1992).

Information on the effects of aging on the anatomy of horizontal, bipolar and amacrine cells is scarce. Curcio and Drucker (1993), counting displaced amacrine cells in human retinal tissue, found no significant age-related changes but admitted that their criteria for identifying those cells were subject to error. Studies on the number of ganglion cells (from counts in the

ganglion-cell layer or the optic-nerve) report a relatively mild overall age-related loss with considerable inter-individual variability (see Spear, 1993, for a review).

Ahmad and Spear (1993) investigated the effects of aging on monkeys' cells of the lateral geniculate nucleus (LGN) as the first major gate of the visual pathway. To my knowledge, no data for humans are available on this issue. They found a statistically significant decrease of neuron density in both the magnocellular and parvocellular layers but no significant loss of neurons. The authors suggested that the decrease in density was a result of an increased LGN volume in old animals (which was also observed in rats; Satorre et al., 1985), due to a significant increase in neuron soma-size and proportional volume increases in the volume of glia cells, blood vessels, and the neuropil (Spear, 1993).

Peters and collaborators (2001) reported changes of the dendritic structure in the primary cortex of elderly rhesus monkeys; relatively few data are available about morphological changes in human striate cortex, though. Scheibel et al. (1975), using Golgi-impregnated material, reported an age-related dendritic loss in human primary visual cortex tissue, which they described, however, as "of relatively less obvious nature" than in other cortical areas they had investigated. Studies on cell density did not reveal substantial differences between tissue samples of younger and older humans (Haug et al., 1984; Leuba & Garey 1987). Similar findings were reported for rhesus monkeys (Vincent et al., 1989).

Concerning extrastriate visual areas, Shefer (1973) found that the number of neurons in layer III of V2 (area 18) was reduced in older humans, with unchanged thickness of the layer. According to Spear (1993), however, these findings had to be interpreted with caution for methodological reasons.More recent brain imaging studies do not speak in favour of a significant volume loss in the occipital cortex of older people (Murphy et al., 1996; Sowell et al., 2003; Raz et al., 2005).

1.4.2. Physiology

Studies on the electro-retinogram (ERG), which is thought to be generated by the retinal ganglion cells, yielded inconsistent results concerning the effects of age. While Tomoda et al. (1991) found little or no age effects in pattern-evoked ERG, other studies (Celesia et al., 1987) reported increases in ERG latencies depending on spatial frequency. Other authors did not confirm changes in ERG latency, but reported age-related modulation of amplitude, independent of spatial and temporal frequencies (Porciatti et al., 1992 Trick & Haywood, 1986). However, when ERG changes were found, they persisted even when optical factors were controlled (for example by the replacement of cataracterous lenses; Porciatti et al., 1992). Spear (1993) commented on those findings that they seem in accordance with the

results from the anatomical observations, that a possible age-related loss of retinal ganglion cells would be rather discrete and quite variable; since the electro-retinographic studies mentioned above were all performed under photopic or mesopic conditions, they would not take into account the finding that most anatomical and morphological changes concerned retinal rods rather than cones, so that more age-related differences might be revealed under scotopic conditions.

Concerning LGN single unit physiology, Spear and colleagues (unpublished results; cited by Spear, 1993) could not evidence substantial differences between young and older rhesus monkeys in a large variety of visual tasks. They commented that this was in accordance with the findings that neither cell number nor morphology in the LGN seemed significantly affected by age.

In a PET study, Grady et al. (1992) tested young and older subjects in a face-matching and a dot-location matching task. In both subjects groups they found the task-typical activation pattern (occipito-temporal during dot-location and superior parietal for face matching) but the occipital activity was generally decreased in the elderly. It furthermore seemed that the functional segregation between the tasks was less pronounced in the older participants. The authors suggested this decrease in functional segregation could be the result of a reduced capacity or efficiency of the extrastriate cortical areas in the elderly, so that supplementary areas would need to be recruited for the different tasks.

Other researchers (using PET and fMRI methods) equally reported an age-related decrease in occipital activity during a variety of tasks, such as lexical decision (Madden et al., 1996), word-pair encoding and retrieval (for example Cabeza et al., 1997, Anderson et al., 2000), temporal-order decision (Cabeza et al., 2000), or working memory (for letters; Rypma et al., 2001). At the same time, many of those studies reported an increase in prefrontal activity in the older participants during these tasks. These findings favoured the assumption that the aging brain would compensate deficits in sensory processing (as suggested by the decrease in occipital activity) by the recruitment of supplementary areas (see Grady et al. 1992, 1994) or cognitive strategies (reflected by the increase in prefrontal activity; see for example Madden et al., 1996, Li & Lindenberger 2002).

Aging has furthermore been associated with a decrease of dopaminergic turn-over (e.g., Bäckman et al. 2000 ; Volkow et al. 1996); the monoamines modulate the cortical signal-to-noise ratio by inhibiting spontaneous background firing and specifically enhancing neural responses to pertinent stimuli (e.g., Mattey et al. 1996). It has been suggested that the age-related decrease of dopamine turn-over would thereby result in an incapacity to suppress non-relevant information (see for example McDowd & Shaw 2000).

Compared to the auditory modality, results about age effects on visual evoked potentials (VEP) are relatively scarce. Most previous EEG studies had focussed on later parts of evoked potentials (beyond 300 ms post stimulus) that rather represent cognitive than sensory processes (see Rossini et al., 2007, for a recent review). Most VEP studies in elderly populations reported a decrease of VEP latencies and amplitudes in older subjects, especially for stimuli with high spatial frequency (Crognale, 2002; Fiorentini et al., 1996; Porciatti et al., 1992; cited by Cepione et al., 2008).

In a recent EEG study, Cepione and collaborators (2008) asked their subjects to react to rare, deviant stimuli (dark blue squares vs. light blue squares as "regular" stimuli). Evaluating the responses to the non-target stimuli, they confirmed earlier findings: VEP amplitudes and latencies were decreased in the elderly for P1 (which is generated in extrastriate visual areas; see for example Clark & Hillyard, 1996), and N1 (which is thought to be produced by multiple generators in the extrastriate cortex and higher order visual areas; see for example Di Rosso et al. 2002). Amplitude differences persisted for P2 (whose functional significance has not yet fully been revealed, but which is likely to represent reactions to the novelty of a stimulus; see Knight, 1997), but latency differences failed to reach significance level.

Oscillatory processes in the brain are thought to reflect cortico-cortial connectivity and are amongst others supposed to play a major role in visual feature binding. It has been observed that aging was accompanied by a decrease of alpha amplitude and a global slowing of the background EEG (see Rossini et al., 2007 for a recent review). Babiloni et al. 2006 confirmed earlier findings and evidenced an age-related power decrease of alpha rhythms in parietal, occipital and temporal regions.

1.4.3. Behavioural data

Age-related alterations of the eye lead (probably due to a reduced retinal illumination; Kline 1987) amongst others to a decrease in visual acuity and contrast sensitivity in older people (Owsley et al. 1983, Weale 1963). A large number of studies have further put forward visual deficits in older observers (see Sekuler & Sekuler 2000, Spear 1993) that cannot be explained by the aging of the peripheral visual system alone (Habak & Faubert 2000).

Elderly people need more time for stimulus encoding, as has been observed in masking experiments (Groth & Gilmore 2003; Walsh 1976); the authors suggest that elderly subjects need more time to "clean" a stimulus at the encoding stage. Older observers also show a diminished temporal fine resolution; compared to young subjects they need a larger time interval for discriminating two successive light stimuli (Misiak, 1949) and also need a larger

time interval between successive stimuli to determine their order of apparition (Poggel & Strasburger 2004, von Steinbüchel 1998).

Scialfa and collaborators (1994) found in a visual search task that elderly subjects had more difficulties in target detection when it was surrounded by heterogeneous distractors – which could be an indicator of a diminished capacity of ignoring non-pertinent information (Scialfa et al. 1994; Scialfa et al. 1998; Gilmore et al. 1985). In visual search tasks the elderly subjects do not normally achieve the same precision level as the young ones, but this effect strongly depends on the presentation duration. It has also been reported that elderly subjects need more time for simple feature extraction (Madden & Allen 1991) and that they are particularly disadvantaged at short presentation times (Scialfa et al. 1998). Other authors reported no particular age-related decreases in feature extraction, but rather in feature binding (Firestone et al. 2007; Kramer et al. 2006). Scialfa and collaborators (1987) found that target detection was complicated when the target was presented in the peripheral visual field. They suggested that elderly subjects were exploring smaller parts of the visual field (diminution of the so-called “useful field of view, UVOF”; see for example Ball et al. 2002; Kosslyn et al. 1999; Sekuler et al. 2000) and that they were taking more time for its exploration. In general, aging seems to be characterized by visuo-spatial attention deficits (Hoyer & Plude 1982; Kramer & Weber 1999). Farkas and Hoyer (1980) suggested that elderly people could perceive a visual scene as composed of smaller perceptual units as young people do; this could account for possible deficits in perceptual grouping but also for the prolongation of response times observed in visual search tasks.

Age-related declines have furthermore been observed in dynamic vision (Wist et al. 2000), motion perception (Betts et al. 2005), motion- or orientation based figure-ground segregation (Kandil & Fahle 2001; Scialfa & Hamaluk 2001; Trick & Silverman 1991), direction discrimination in texture segregation tasks (Ball & Sekuler 1986), integration of local orientation information across space (Del Viva & Agostini 2007; Roudaia et al. 2008), and closed contour integration (McKendrick et al. 2010).

To our knowledge, the perception of ICs has itself not yet been investigated explicitly in older populations. Among the different paradigms presented here, those of contour integration seem most related to our central theme, the perception of ICs. In contour-integration tasks subjects are to detect contours comprised of local features that are embedded in cluttered backgrounds (Field et al. 1993). McKendrick and collaborators (2010) reported that older subjects could not link the elements constituting the shape over the same distances as young subjects.

In most cases it seems that the observed deficits in visual processing in older adults are not qualitative in nature, i.e., subjects perform the tasks with almost the same accuracy as young subjects do. Their behaviour is, however, mainly characterized by a slowing in response behaviour, which could to some extent be explained by the general slowing of information processing in aging (Salthouse 1991; Cerella 1985; Birren 1965). Other possible explanations for the slowing-down of visual (and cognitive) information processing in aging were suggested on the level of attention: difficulties in performing double-tasks (McDowd & Shaw 2000) and failure to suppress non-relevant information (McDowd & Shaw 2000). The interference of non-pertinent information results would result in an additional charge on the processing systems, thereby prolonging response times.

2. Aims of the study

Kanizsa figures are often used in clinical neuropsychological studies (e.g., Conci et al. 2009; Grabowska et al. 2001; Vuilleumier et al. 2001; Mattingley et al. 1997) or standard clinical neuropsychological screening for dementia. In the latter, a Kanizsa-type graphic is shown to the patient, who is then asked what he can see in this picture. The patient is supposed to perceive the Kanizsa illusion; if this is not the case, gnostic problems are suspected. The underlying assumption is that the perception of ICs is not affected by normal brain aging. However, no systematic research has as yet been conducted on this completion mechanism in normal aging. The above mentioned testing of IC perception in the clinical context is for example performed without time limit, which means that perceptual deficits could remain undiscovered because of the presence of compensatory mechanisms. Moreover, it cannot always be excluded that the seeming detection of an IC by a patient or a healthy elderly person is just the result of a suggestive question posed by the investigator.

Data from functional imaging (for example Grady et al. 1994), showing less efficient use of the cortical areas implied in IC perception in old subjects, as well as behavioural data – for example from feature-binding (e.g., Firestone et al. 2007; Kramer et al. 2006) or contour-integration experiments (McKendrick et al. 2010) – lead us to suppose that IC perception could also be altered through the normal aging process.

The primary goal of this dissertation therefore lies in characterizing the perception of illusory contours in elderly subjects. In an explorative approach, we intend to obtain behavioural as well as electrophysiological measures of IC processing in healthy older adults and young control subjects.

3. Experiment 1–4

3.1. Experiment 1 – Perception of ICs in young and elderly observers (psychophysics)

3.1.1. Subjects

A total of 113 unpaid volunteers took part in this experiment. Participants had been recruited via message boards at Geneva University from the staff of the Geneva University Hospitals, classes of the ”University of the Third Age” in Geneva, and from local sport clubs. Subjects were subdivided into four age groups: from 18 to 30 years of age (Group 1), 31 to 50 years (Group 2), 51 to 70 years (Group 3), and from 71 to 90 years (Group 4) (see Table 1 for details). All participants were native French speakers, and right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971).

Group	***n***	***Age (sd)***	***Gender***
1: 18-30 years	29	23.9 *(2.6)*	12m, 17f
2: 31-50 years	18	43.7 (*5.3*)	5m, 13f
3: 51-70 years	27	65.1 (*4.1*)	3m, 24 f
4: 71-90 years	39	77.6 (*4.8*)	11m, 28f

Table 1: Demographic data of participants in Experiment 1

Inclusion / exclusion criteria

Visual acuity: Visual acuity was assessed for far vision (with a Snellen E-chart) and near vision (plastic reading card with continuous text in different font sizes; © Ryser Optics; St. Gallen; Switzerland). To be included, subjects had to attain a visus of 0.8 or better (16/20; with normal or corrected-to-normal vision). Contrast sensitivity was tested with a low-contrast flip chart (© Precision Vision, Illinois, USA). The criterion for inclusion was set to 10% but all participants showed a contrast sensitivity of 5% or better (1/Michelson contrast).

Psychoactive medication: Subjects were not to take any medication that might affect test results (i.e., neuroleptics, anti-depressants etc.).

Cognitive status, neurological or psychiatric disorders: Subjects were not to present any history of psychiatric or neurological disorders. To exclude the possibility of a beginning cognitive decline, elderly subjects passed a neuropsychological battery comprising tests for memory (Grober & Buschke 16-items; Buschke et al., 1997; direct and inverse digit span;

Wechsler, 1981; Corsi Block tapping test; Corsi, 1972), word fluency (Borkowski et al., 1967), processing speed (digit symbol substitution test; Wechsler, 1981), and intelligence (Mill Hill Vocabulary Scale; Raven, 1938). All elderly subjects performed within their age norms.

Education: All participants had a minimum of 7 years of formal education.

Prior to testing, the participants were informed about the purpose of the study and gave their written consent.

3.1.2. Stimuli and procedure

The following experiment has been elaborated in the context of project "Temporal Processing in Brain Aging and in Patients with Alzheimer's disease" (granted to Prof. Dr. Nicole von Steinbüchel by the Swiss National Fund for Scientific Research; SNFR 31.66806-01) and was programmed by Dipl. Ing. Torsten Wuestenberg (University of Göttingen) using the psychological experimentation software Presentation (© Neurobehavioral Systems, USA; version 0.71). Statistical analyses were performed with SPSS for Windows (version 15.0).

Stimuli in this task comprised two types of real contour triangles, two types of non-shapes, and one type of IC-triangles (see Fig.5).

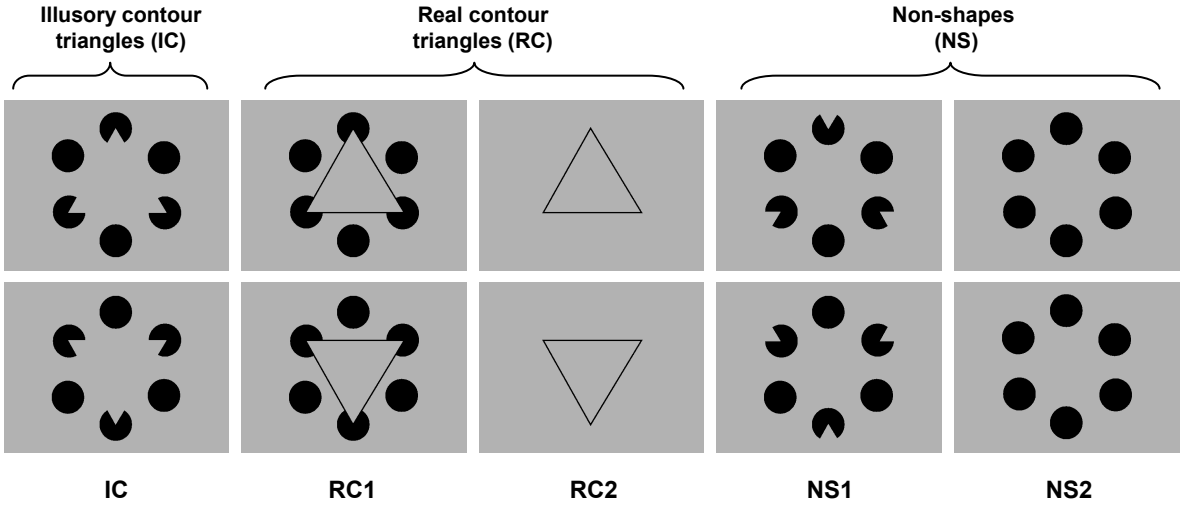

Fig. 5 : Perception of illusory contours ; psychophysical experiment : stimuli

The stimuli were variants of the well known Kanizsa illusion where a shape like a triangle is seen in front of patches, called inducers. All stimuli except the pure real-contour triangle contained 6 inducer discs of 6° diameter each, arranged in a circle around the centre of the computer screen. The distance between disc centres subtended approximately 10° of visual angle. In the IC-condition, a 60° inward-facing sector was cut out of each of three (non-neighbouring) inducer discs ("pacman"-inducers), as to give rise to the illusion that an equilateral triangle of 17° side length was spread across the centres of the three pacman-

discs (the support ratio corresponding to 0.36). In the RC1 condition, the outline of the triangle connecting the centres of three of the inducer discs was actually drawn (0.3° line thickness). The RC2 condition consisted of the same equilateral triangle as in RC1 but without the inducer discs. In the NS1 condition, the pacman inducer discs pointed outwards, so no illusory shape would be perceived. In the NS2 condition, finally, only the six complete inducer discs were presented.

The tip of the triangles could either face upwards or downwards, excluding the possibility that a decision (about the presence or absence of a triangle) could be made by fixating one inducing element alone.

Stimuli were black (0.36 cd/m^2) and were presented on a light grey (75 cd/m^2) background of a 15'' LCD screen. Specific care was taken to ensure that the viewing angle between observers and screen was perpendicular. Viewing distance was approximately at 40 cm from the screen.

Each stimulus type (IC, RC, NS) was presented 36 times in a pseudo-randomized order. A relatively short stimulus presentation time (218 ms) was chosen to avoid ceiling effects. Subjects were instructed to fixate the centre of the screen and keep their left and right index fingers above two marked buttons of the keyboard. They pressed the right key when they perceived a triangle (RC and IC) in the centre of the screen, and the left key when they saw no triangle. They were informed that response times were assessed and were asked to respond as quickly and accurately as possible.

Before the actual experiment started, subjects passed a short training phase in which all the various stimulus types were presented without time limit. The experimenter verified that subjects understood the instructions and pressed the buttons correctly. If necessary, it was pointed out again that illusory triangles would equally count as triangles.

The experiment was performed in a quiet, dimly lit room. Each of the 108 trials was started by the experimenter by pressing a mouse button. The time interval between two trials was approximately three seconds, resulting in a total duration of around 6 minutes for the entire experiment.

Data processing

For each participant, the median response times (being less susceptible to outlier values) per condition (from correctly answered trials only), and percentage of errors per stimulus condition were calculated. To separate stimulus-specific slowing effects from general slowing, median response times were then normalised to RC2 (as 100%).

Statistical analysis was based on a 4 (age group) x 5 (stimulus) repeated measures ANOVA. Three separate analyses were performed: a) absolute reaction times, b) reaction times with RC2 as 100% reference, c) error rates (in %).

3.1.3. Results

a) Response Times

Group means of participants' median response times before normalization are displayed in Figure 6 and Table 2.

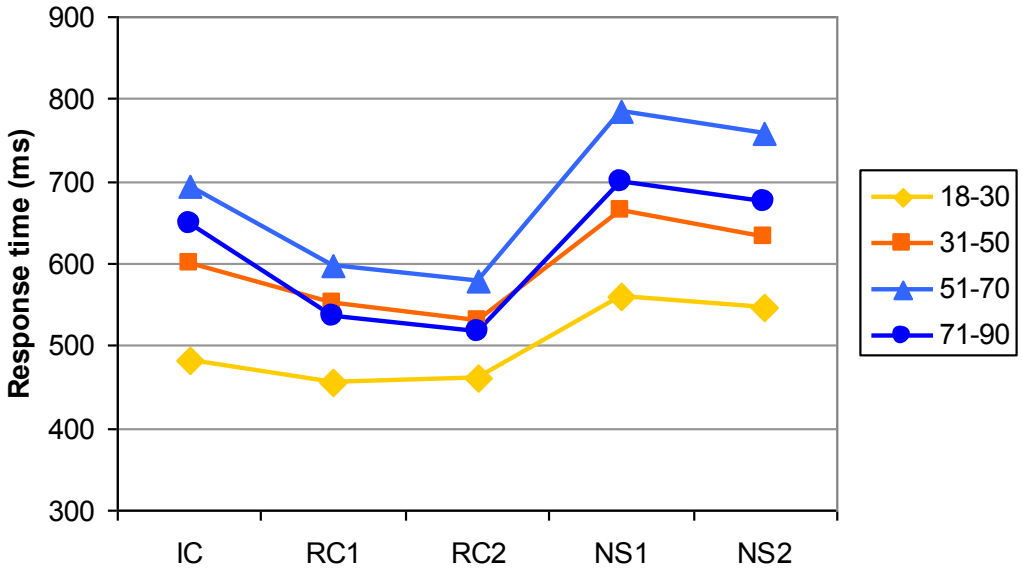

Figure 6: Mean response times per age group and condition

	IC *Mean* *sd*	***RC1*** *Mean* *sd*	***RC2*** *Mean* *Sd*	***NS1*** *Mean* *sd*	***NS2*** *Mean* *sd*	***All conditions*** *Mean* *sd*
18-30	483.4 *112*	456.4 *138*	460.0 *103*	560.0 *133*	546.7 *145*	515.0 *126*
31-50	600.7 *142*	551.0 *107*	529.4 *128*	664.3 *146*	632.9 *128*	605.8 *132*
51-70	692.6 *175*	597.2 *116*	579.1 *123*	784.3 *199*	758.4 *184*	701.4 *230*
71-90	647.4 *169*	535.7 *126*	516.7 *118*	697.8 *179*	674.7 *153*	629.5 *167*

Table 2: Group means of individual median response times per condition

Independent of stimulus condition, participants' response times increased with age ($F_{(3,109)}$ = 7.68; p<.001; $mean_{group1}$ = 501ms; $mean_{group2}$ = 596ms; $mean_{group3}$ = 682ms; $mean_{group4}$ = 614ms). However, post-hoc t-Tests (Bonferroni-adjusted) revealed that only response times for the youngest participant group were significantly faster than those in the three remaining age groups. As expected, we observed a significant stimulus effect ($F_{4,436}$= 119.1, p<0.001). *Post-hoc* analyses (*LSD*) revealed significant differences between all stimulus conditions

except for the two real triangles RC1 and RC2, with the two real triangles (RC1 and RC2) leading to the fastest reaction times and the triangle-absent condition with pacmen inducers (NS2) to the slowest (all p<.005).

To separate stimulus-specific age effects from a general slowing, group means of subjects' median reaction times were normalised to the condition with real triangles without inducers (RC2) serving as baseline, and plotted in Figure 7.

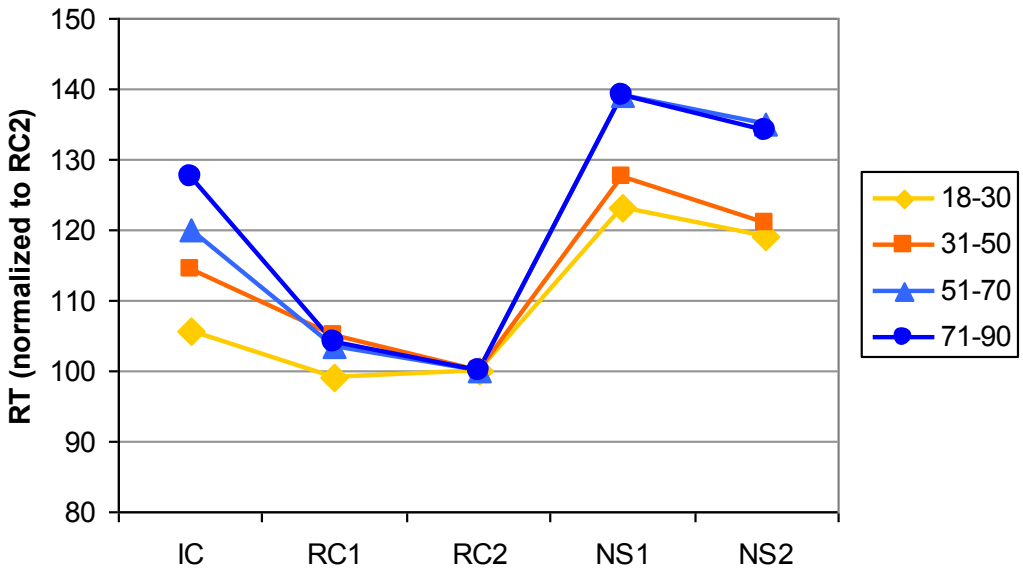

Figure 7: Response times per age group and condition, normalized to RC2

A significant interaction between age group and stimulus condition based on repeated measures of normalised RTs ($F_{12,436}$= 3.321; p<0.001) revealed that young participants did not show any RT differences between illusory contour stimulus and real triangles, whereas all other age groups responded significantly slower to the presence of an illusory than to real triangle. This difference was largest for the two upper age groups, with the oldest age group showing the largest increase in reaction times for IC as compared to RC1 and RC2.

b) Error rates

As can be seen in Figure 8, error rates in this task were generally low. They increased, however, significantly with age ($F_{(3,109)}$ = 5.21; p<.005) from 1.6% in the youngest age group to 4.1% in the oldest). Further, they differed significantly between stimulus conditions: significantly fewer errors were made for the two real triangle conditions (around 1.6%) than for the three remaining conditions IC, NS1 and NS2, where the latter did not differ from each other (between 2.9% and 3.3%).

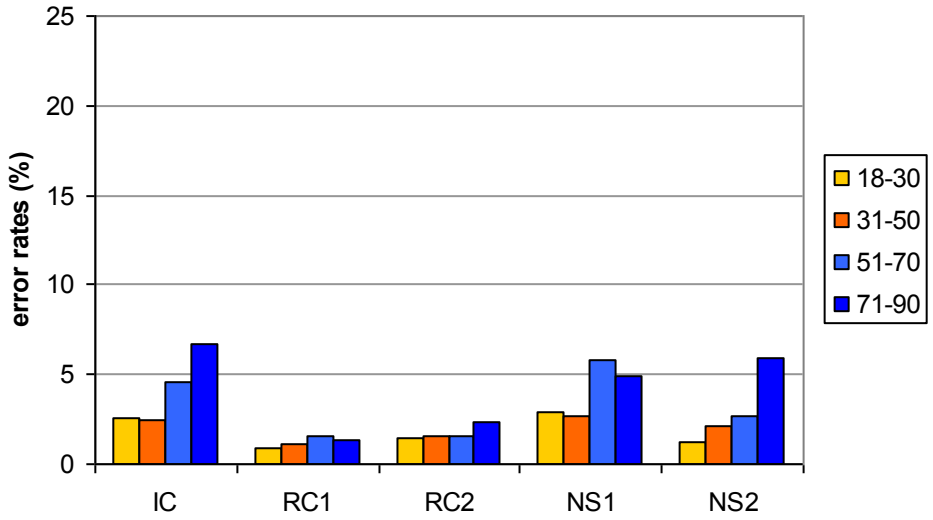

Figure 8: Average error rates (%) per age group for the five stimulus conditions

Even though the interaction between age group and stimulus condition only approached significance (F=1.647; p=.078), a *post-hoc* analysis (Bonferroni-adjusted) of error rates revealed that only the oldest age group made significantly more errors for illusory contours and non-shapes with filled inducers (NS2) than the youngest age group.

3.1.4. Discussion

Our results confirm the general increase in response times in elderly populations which has been reported oftentimes for a variety of tasks (see for example Verhaeghen and Salthouse 1997 for a review). It is furthermore well known that the decision about the presence of a target can generally be made quicker than the decision about the absence of a target (see for example Treisman & Gelade, 1980). It is thus not surprising that response times for the two non-shapes NS1 and NS2 were slower than for the conditions RC1, RC2, and IC, in which the target ("triangle") was present; especially since the proportion of trials containing triangles was bigger than the proportion of trials without.

More interesting however, is the finding that the aging process seems to go hand in hand with increased difficulties in the identification of IC figures. While it seemed that for young subjects it hardly makes any difference whether a triangle was bound by real or illusory contours, the proportion of additional time required by the elderly observers for the IC stimuli steadily increased with increasing age.

To the present day, no studies on the perception of IC in older populations have been published; the only indications stem from clinical background: Kanizsa figures are sometimes presented in neuropsychological testing. The examined subjects are examined whether they

perceive the Kanizsa illusion; when not, visual agnosia is suspected. Underlying this practice is the rationale, that the perception of IC should not be affected by normal brain aging. Our data suggest, however, that even though the capacity to perceive IC may not be lost with advancing age (indicated by the low error rates), there seems to be a slowing of the implicated processes.

It has been reported that elderly subjects needed more time for simple feature extraction in visual search tasks (Madden & Allen 1991) and that they were particularly disadvantaged at short presentation times (Scialfa et al. 1998). Stimulus durations in those studies that led to a noteworthy decline in elderly subjects' performance (less than 100 ms in Scialfa et al.) were, however, considerably shorter than in our experiment (>200 ms), so stimulus presentation duration seems rather unlikely to account for our observations.

Another possible explanation for the increased difficulty in IC perception in case of the older observers could be the relatively large stimulus size we used. It has frequently been reported that target detection was complicated for older observers when the target was presented in the peripheral visual field (Scialfa et al. 1987), or, generally spoken, there was an "age x eccentricity" effect (for example Coeckelberg et al. 2004), or a diminuition of the "useful field of view" (UFOV, see for example Kosslyn et al. 1999; Sekuler et al. 2000). Because of this presumed age-related reduction of the UFOW and the large stimulus size we used, elderly subjects might have more difficulties in binding the elements that compose the illusory figure into a coherent shape than do young subjects.

Finally, we wanted to rule out the possibility that group differences in this task were simply caused by an age-related diminution of general vision parameters. Due to the strict inclusion criteria we had applied concerning near and far sight, as well contrast sensitivity, we could however not evidence any correlation between these measures and task performance.

3.1.5. Conclusion

It is still heavily debated whether IC perception is rather a simple "bottom-up process" or whether higher, cognitive "top-down" processes play an important part in building the percept. Some authors have, for example, reported that IC figures could be detected in parallel search in visual search tasks (Davis & Driver 1994). Yet, if IC perception was a purely automatic process, how could this explain our findings that older subjects have apparent difficulties (indicated by prolonged response times) with these stimuli compared to RC figures?

As a first step we wanted to see whether we could find an electrophysiological correlate to our observations. Would there be observable differences in IC processing between young and old subjects in EEG? To this purpose we designed Experiment 2 which is presented below.

As a second step we wanted to make sure that the group differences we found were not the result of older subjects' impaired visual processing at higher eccentricities of the visual field. In Experiment 3 (see Chapter 3.3) we investigate the influence of stimulus size by contrasting (in a within-subject design) the replication of this psychophysical experiment (with relatively large stimuli) with a second experiment, which is identical in procedure, but using a smaller set of stimuli.

3.2. Experiment 2 – Perception of ICs in young and elderly observers (EEG)

3.2.1. Subjects

Subjects for this EEG-experiment were recruited among the participants who had passed Experiment 1, so the same inclusion / exclusion criteria were used here. Being particularly interested in possible IC processing deficits in advanced age, we only composed two (instead of four) age groups, the younger one ranging from 21 to 27 years of age, the older one from 57 to 82 years (see Table 3 for details).

Group	***N***	***Age (sd)***	***Gender***
1: 21-27 years	19	23.7 *(2)*	9m, 10f
4: 71-90 years	22	70.6 *(6)*	6m, 16f

Table 3: Demographic data of participants in Experiment 2

3.2.2. Stimuli and procedure

The experiment was performed in a sound-attenuated, dimly lit room. Three different stimuli were presented in the EEG paradigm: one RC, one IC and one NS (see Fig. 9). Stimuli were basically composed in the same way as the ones used in the psychophysical paradigm, with circular inducer discs, a real or illusory triangle of 6° side length, or outwards pointing pacman inducers in the NS condition, respectively. Inducer discs subtended 1.4° in diameter; the side-length of a (real or illusory) triangle was approximately 6° of visual angle, the support ratio 0.24. The line thickness of the real contour triangle corresponded to 0.09° of visual angle. A fixation cross (around 0.14° of visual angle in diameter) was placed in the centre of the screen, which remained there throughout the whole experiment. As in the

psychophysical paradigm, stimuli were black (0.36 cd/m^2) and appeared on a grey (75 cd/m^2) background of a 17'' monitor which was placed at 160 cm viewing distance from the observer.

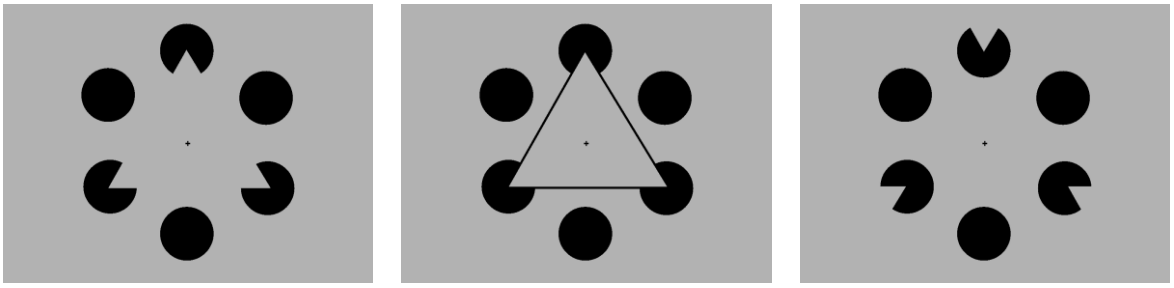

Fig. 9: Perception of illusory contours ; EEG experiment : stimuli

The experiment was a "non-response paradigm", i.e. no manual response was required from the subject in the acquirement of the evoked response. Subjects were seated in a comfortable chair and were asked to focus on the fixation cross and, if possible, avoid any movement.

Stimuli were presented for 500 ms, followed by a blank screen with only the fixation cross. Time between two successive presentations was fixed at 1000 ms. Stimuli were presented in a pseudo-randomized sequence; each of the three stimulus types shown at least 200 times. To avoid fatigue, the recording was subdivided into eight blocks, the duration of each not exceeding 2 minutes.

Recording parameters

Continuous EEG was recorded at a 500 Hz sampling rate with a Hydrocel Geodesics Sensor net (Electrical Geodesic Inc., Oregon, USA) acquisition system, from 125 electrodes referenced to the vertex. In this system the electrodes consist of little sponges which are attached to a net and soaked in a conducting fluid (water, salt, and shampoo). The net is then placed on the surface of the scalp. Placing the net requires about 10 minutes by an experienced experimenter.

Three electrooculogram leads (EOG) were used to monitor eye movements. The EEG was filtered offline from 1 to 30 Hz and recalculated against the average reference (Lehmann and Skrandies, 1980). Data analysis was performed with the CarTool system developed by the Functional Electrical Imaging Laboratory of the Geneva University Hospitals (CarTool 3.2.2.0; © Denis Brunet 1996-2004).

Data processing

Averages (i.e. visual evoked potentials, VEP) were computed separately for each subject and each condition, epochs lasting from 400 ms before to 600 ms after stimulus onset. All epochs were inspected for artefacts and trials containing artefacts (eye movements or electrode drifts) were rejected. The remaining trials were subjected to a base-line correction (electric activity level 50 ms before stimulus onset serving as base-line) and normalized for global field power (GFP) to account for inter-individual differences in signal strength.

To gain a first impression of possible stimulus effects in the different subject groups, t-tests (for dependent samples) were performed for each amplitude at each time frame on the grand means (mean VEP of a group for one condition), between the conditions RC vs. IC, RC vs. NS, and IC vs. NS (see Fig. 12). This was done to determine in which temporal windows differential reactions would occur and which electrodes were implicated. Moreover, a t-test for dependent samples was applied for testing the time course of differences in global field power (GFP) between conditions. The programs for the t-tests (for amplitude and GFP) were developed by Prof. Christoph Michel from the Functional Electrical Brain Imaging Laboratory of the Geneva University Hospitals.

Two types of analyses were conducted subsequently:

Map series analysis of the VEP: Map series analyses will be performed primarily with the standard methods from the Functional Electrical Brain Imaging Laboratory. In a first step, the grand means (mean VEP for all participants of a group) will be determined for each condition in the two groups (young/old). On the basis of these data, a segmentation of the different spatial configurations ("micro-states") across time will be effectuated (comparable to a cluster analysis). This type of analysis is based on the idea that changes in the map configurations correspond to changes in the underlying active neural populations (Pasqual-Marqui et al. 1995). The aim of this procedure is to explain, with an optimal number of maps of spatial configurations, a maximum of the observed variance in the EEG signal. In a next step, differences between conditions can be compared; for example, if an electrophysiological reaction to a RC stimulus is different to the reaction to an IC stimulus, different maps will be chosen to explain the reactions in the two conditions. Moreover, individual VEP can be compared to the grand means of a group, by calculating for the different maps a spatial correlation coefficient which represents a measure of "goodness of fit". Furthermore, statistic calculations can be performed with this index, for determining group effects, condition effects and interactions. In a preceding descriptive analysis we will determine by temporal window (the temporal windows corresponding to the P100, N150 and P200 are currently considered; modifications are possible, according to the data), which of the maps explains the maximum of variance observed in a group. Subsequently, the individual "goodness of fit" index for this

map (by temporal window and by condition) will be determined. To find out for example whether different maps are predominant in the two groups in a given condition, the goodness of fit index can be subjected to repeated measures ANOVA, for testing group (young/old) and condition (RC/IC/NF) effects and interactions (group x condition).

Peak analysis of the VEP: The amplitudes (in µV) and latencies (in ms) of the VEP peaks P100, N150 and P200 of each subject were determined by visual inspection for six representative electrodes: O1 and O2 for occipital, P3 and P4 for parietal, and PO7 and PO8 for parieto-occipital sites. In a second step, amplitudes and latencies of the peaks were submitted to descriptive statistics and subsequently tested with a MANOVA for *condition* effects (RC/IC/NS), *group* effects (young/old), *position* effects (occipital/parietal/parieto-occipital), *side* effects (left/right hemisphere) and possible interactions.

3.2.3. Results

To gain a first impression, Figure 10 shows the superimposed grand averages of young (Fig. 10.a) and old (Fig. 10.b) observers for the conditions RC (black lines), IC (red lines), and NS (green lines), from stimulus onset to 600 ms post-stimulus. Note that GFP-normalized VEPs are presented here to control inter-individual differences in signal strength, so no direct comparisons of VEP amplitude between groups should be drawn.

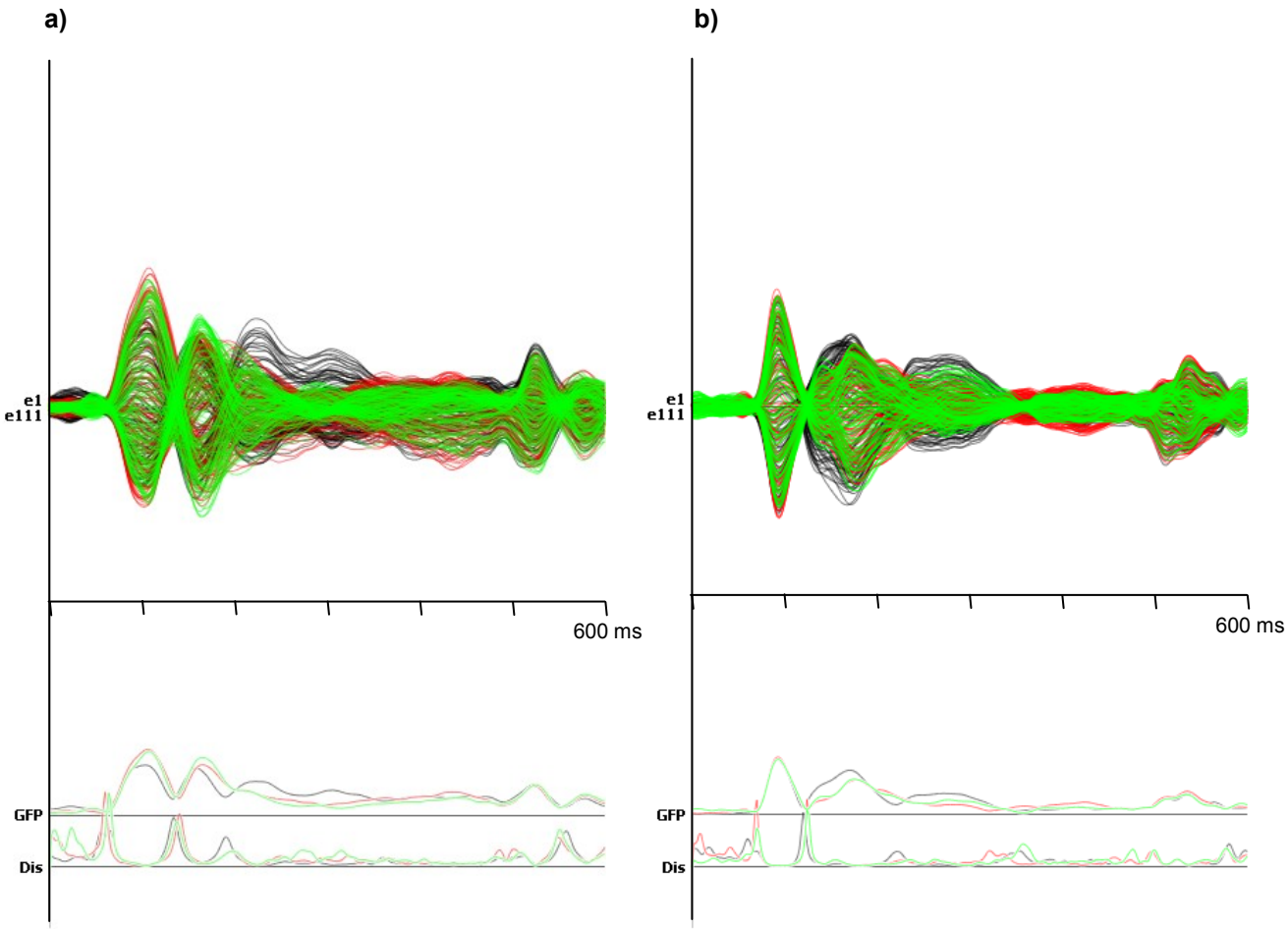

Figure 10: Grand averaged VEPs of all electrodes for young (a) and older (b) participants, for the conditions RC (black), IC (red), and NS (green). Bottom lines: GFP: global field power; Dis: dissimilarity between maps (dissimilarity peaks when maps change, for example at the transition from the P100 to the N150).

Visual inspection of these potentials reveals a first major burst of activity around 100 ms post stimulus (corresponding to the P100) and a second around 150-180 ms post stimulus (corresponding to the N150). A third noteworthy increase of activity only emerges for RC stimuli, around 220 ms post stimulus in young, and around 270 ms in older observers. Furthermore, while RC responses apparently differ from IC and NS in waveform and GFP, differences between IC and NS seem marginal.

Figure 11 shows grand averaged ERP waveforms for ten representative electrodes at different scalp positions (Fp1, Fp2, C3, C4, P3, P4, T3, T4, O1, O2) for young (Fig. 11.a) and old (Fig. 11.b) participants.

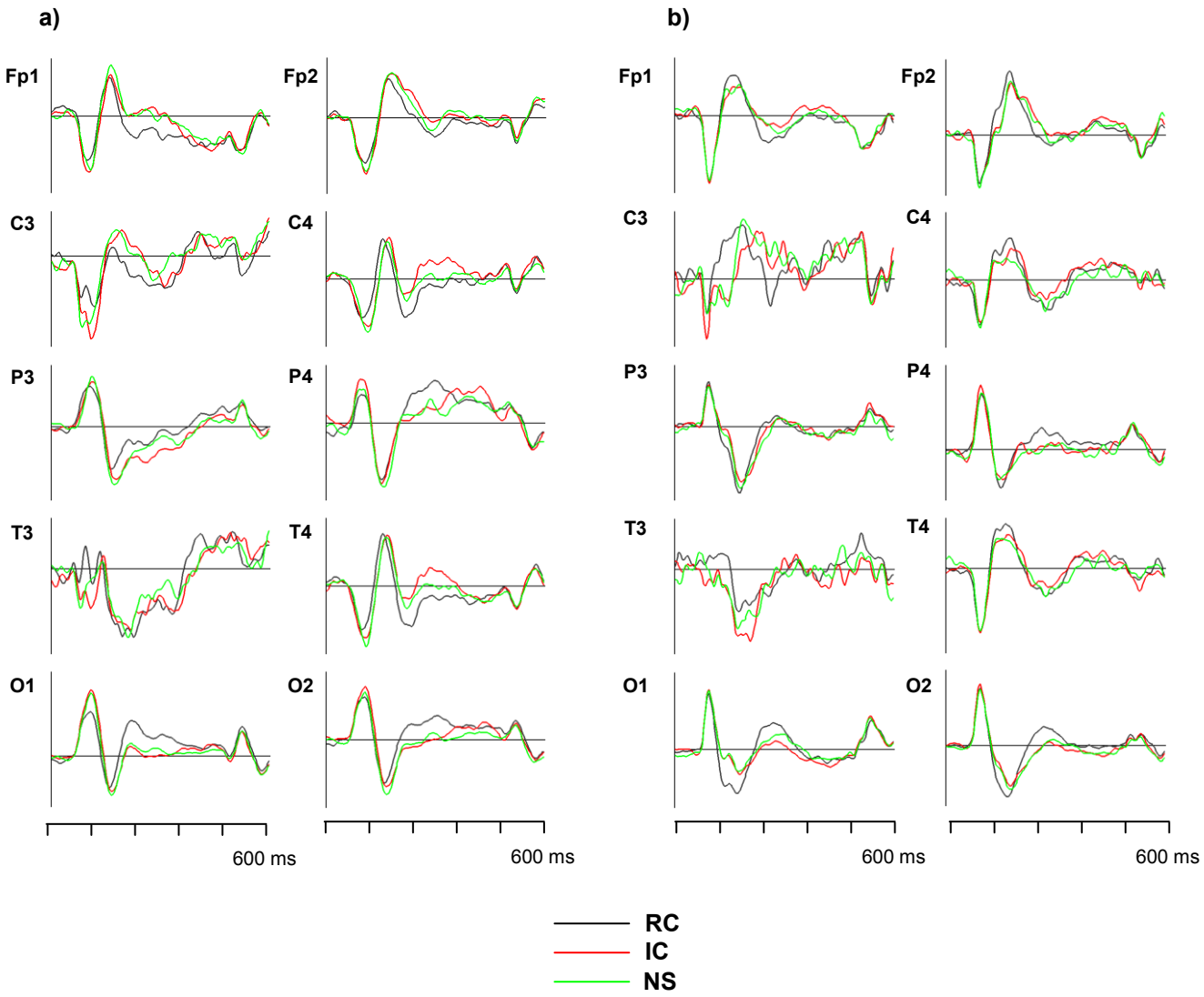

Figure 11: grand average ERP waveforms of young (a) and old (b) participants for the conditions RC, IC, and NS for ten selected electrodes (positive polarity shown upwards).

Visual inspection of these waveforms confirms that there are only small differences in amplitude or latency that can be observed between IC and NS in both groups.

T-Test on VEP amplitude over time

As a next step, we performed pair-wise t-Tests of VEP amplitude between two conditions at a time, across all electrodes and time sample points, to obtain a general idea of the temporal periods during which differential reactions would occur. Results are displayed in Figure 12:

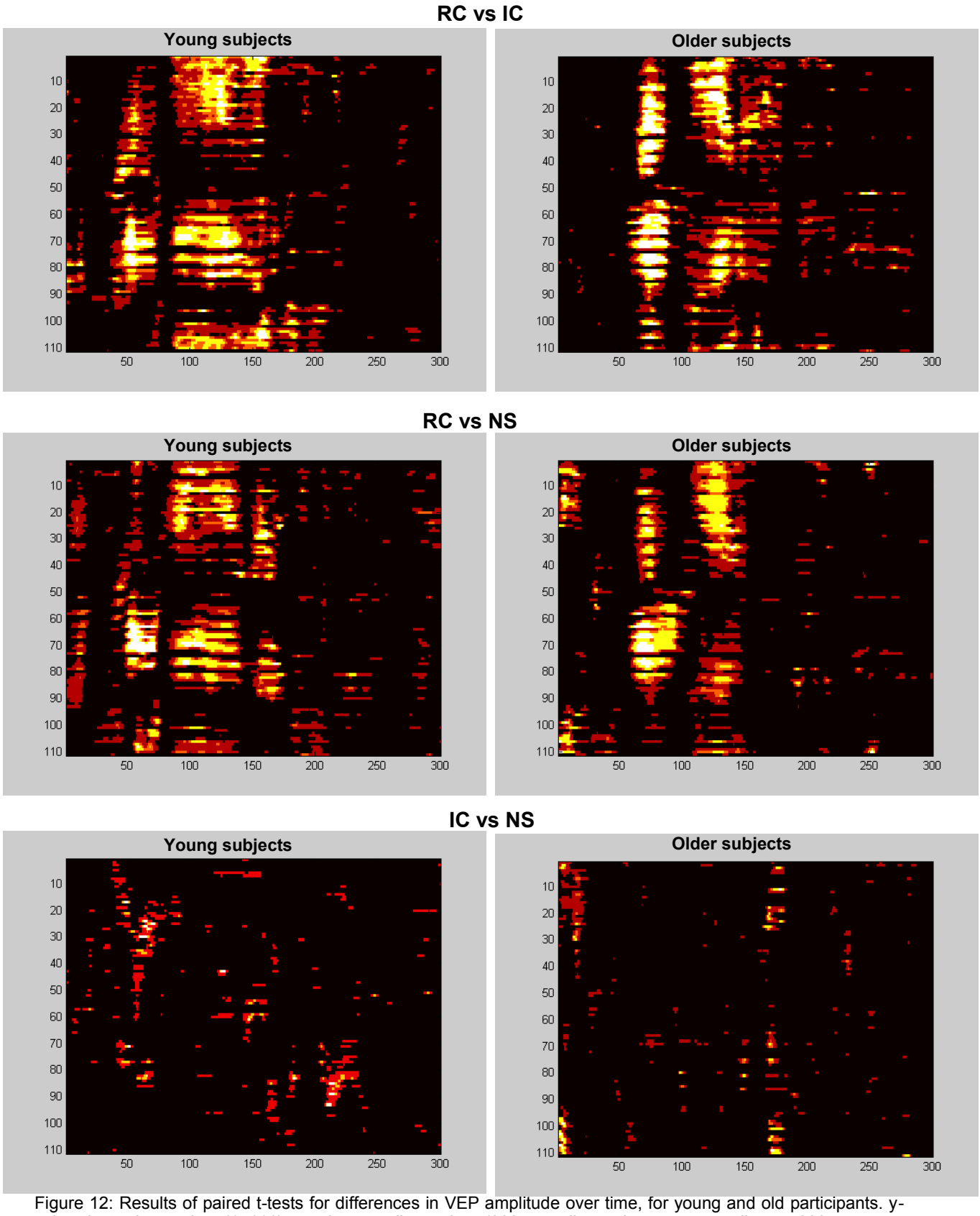

Figure 12: Results of paired t-tests for differences in VEP amplitude over time, for young and old participants. y-axis: electrode number (1–111); x-axis: sampling points (300 sampling points corresponding to 600 ms post-stimulus). Significance level is indicated by increasingly brighter colour: black: not significant; red: $p<0.05$; orange: $p<0.01$; yellow: $p<0.005$; white: $p<0.001$).

Statistical analysis confirms our observations above: while there are remarkable differences in VEP wave-form between RC and IC or NS in both groups, there are little to no differences between IC and NS. Comparing young to older observers, the first noteworthy differences between RC and the other conditions appear around 100ms post-stimulus in the young, but only around 150ms post-stimulus in the older group. A second epoch with statistical differences in VEP amplitude in the RC-condition occurs in both groups around 200 to 300 ms post-stimulus.

As depicted in Figure 12, differences between IC and NS are marginal. A slight differential reaction is observed in young participants around 100 to 150 ms and around 300-500 ms post-stimulus. Elderly participants do not exhibit an early differential reaction but a short period of significant amplitude differences around 350 ms post-stimulus.

In some comparisons, Figure 12 displays some very early differential reactions. It should however be noted that these occurred during low VEP-amplitude periods shortly after stimulus presentation; most likely, these early differences can be disregarded.

Map series analysis

As a next step, we wanted to investigate whether the differences we observed between conditions are due to differences in scalp topography of the VEP or rather to differences in the amplitude of the evoked electrophysiological response. We applied a method developed by Murray et al. (2004) that identifies periods of stable electric field topographies (so-called microstates) based on a spatial clustering algorithm that allows determining dominant electrical field topographies and their evolution over time. Results are displayed in Figure 13:

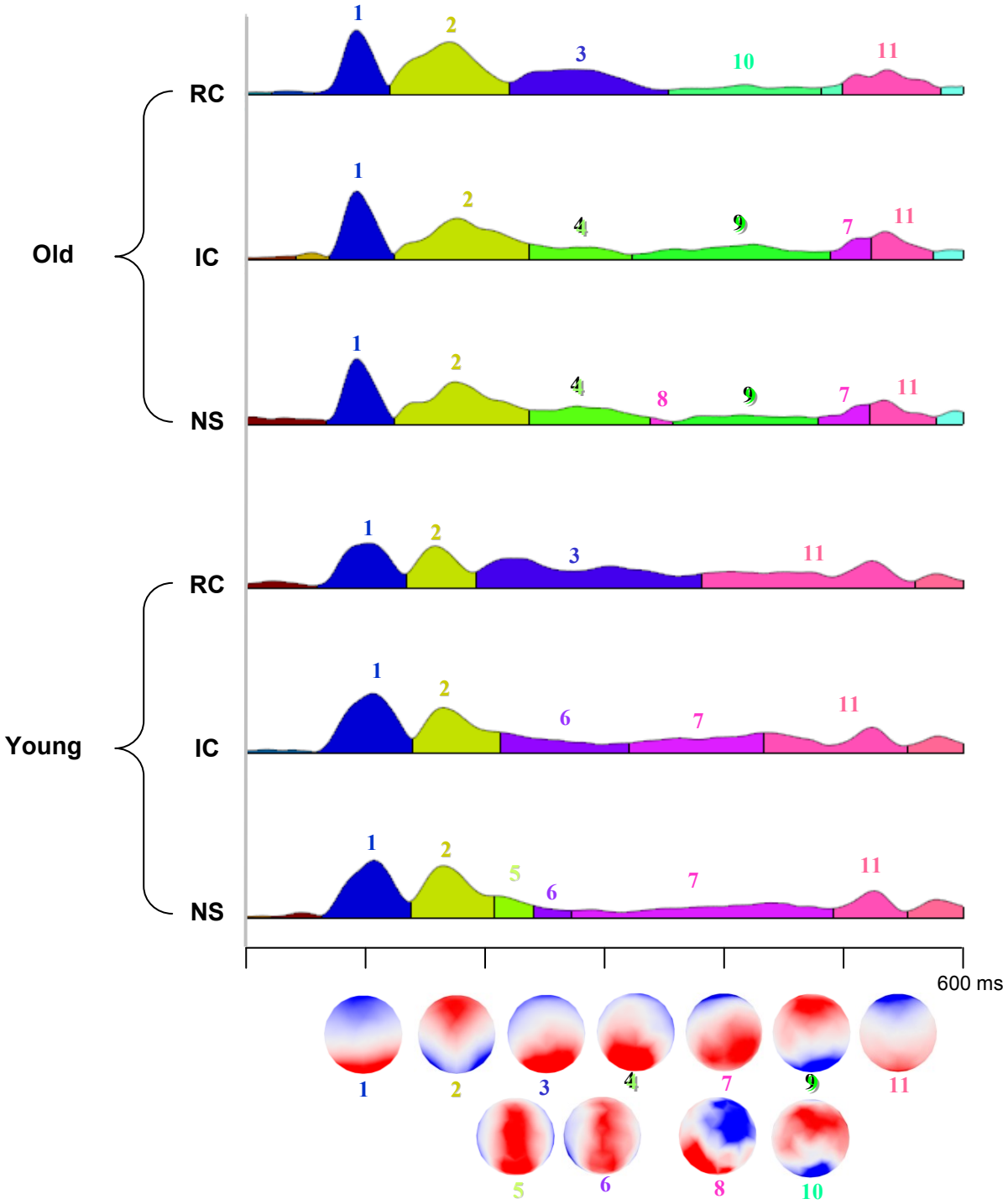

Figure 13: Results of map-series analysis for global field power in young and older observers for the conditions RC, IC, and NS. The time segments of stable field topography in the six traces are highlighted with different colours under the global field power curve. Corresponding field topographies (for periods of sufficient general GFP-activity) are shown below.

Our results indicate that the topographies of the early ERP-components, P100 and N150, do not differ between conditions, or between young and old subjects. First differences appear around 200 ms post-stimulus, predominantly between RC and IC/NS. In the RC condition, the N150 is followed by a map with positive occipital polarity (similar to the P100) in both groups. While in the group of older subjects the N150 in the IC and NS condition is followed

by a field configuration of negative occipital polarity before turning into an inverse pattern around 550 ms post-stimulus, younger participants rather exhibit a parietal pattern of activation. The field configurations for the latter ERP-components should, however, be interpreted with caution since they occur during periods of relatively low GFP.

Figure 13 furthermore shows that neither young nor older participants exhibit a special cortical map for IC, which would have indicated that a particular brain area were exclusively responsible for the processing of ICs. Similar results have been reported previously (see for example Pegna et al., 2002).

If, therefore, the physiological distinction between IC and NS cannot be explained by differences in topography, other mechanisms must account for differential reactions which allow shape detection.

Analysis of GFP

As a next step we tested whether the distinction between shapes might be drawn upon differences in GFP between conditions. Individual GFP values were calculated for all sampling points (from 0 to 600 ms post-stimulus) and submitted to pair-wise t-Tests between conditions RC/IC, RC/NS, IC/NS. Analyses were performed separately for young and old subjects. Results are displayed in Figure 14:

Figure 14 reveals that young and older observers do not seem to process shapes in the same way. As in our t-Tests for ERP amplitude, significant GFP differences between conditions occur already around 100 ms post stimulus in the young participants, while no differential reaction can be found in the older subjects until around 150 ms post stimulus. In case of ICs vs. non-shapes, significant GFP differences occur no sooner than around 250 ms post stimulus.

While the perception of RCs compared to other stimuli goes along with lower GFP in younger subjects (which has been reported previously, see Pegna et al. 2002), older subjects' GFP is higher for RC than for other conditions. That increase in GFP could reflect (as intended) the complexity of the shape that needs to be encoded. It should be kept in mind, though, that the RC stimulus differs slightly from ICs and NSs in terms of the dark-/ light proportions of the stimulus pattern, therefore not allowing to exclude effects of luminance and contrast from the visual / cognitive shape processing in interest. In the comparison of ICs vs. non-shapes (with equal dark-/ light proportions of the stimuli), however, both young and old subjects show only feeble GFP differences.

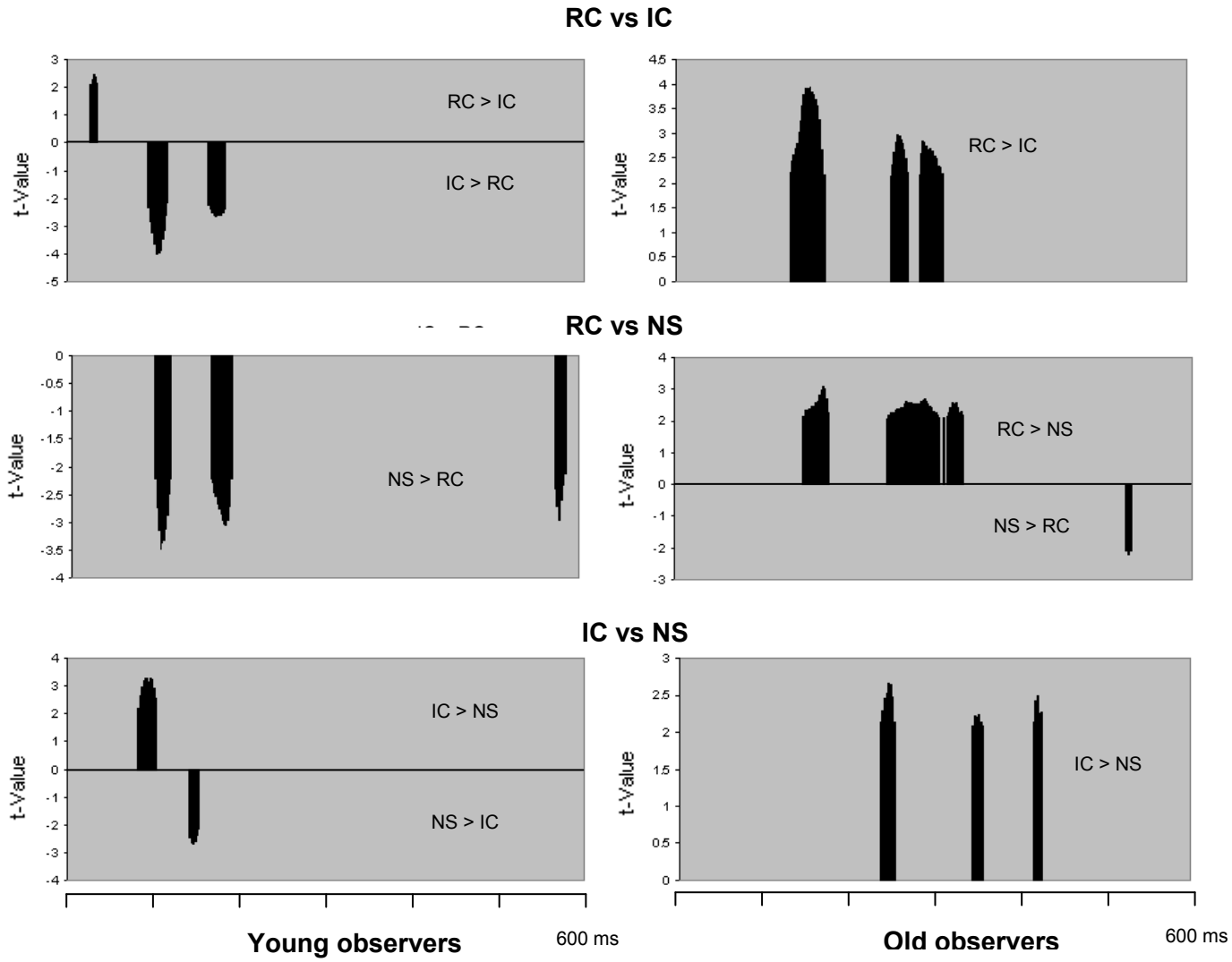

Figure 14: Results of paired t-Tests of GFP between conditions for young and old observers. Only statistically significant values ($p<0.05$) over a period of more than 10 ms are shown. Y-axis: t-Value; X-axis: time post stimulus (ms).

Analysis of peak amplitudes and latencies

As a next step, we were interested whether the differences we had observed between conditions (in our t-Tests for amplitude and GFP) were the result of actual differences in ERP amplitudes, or were rather the result of condition-related delays of one or more ERP components. Amplitudes and latencies of ERP components P100, N150, and P200 were ascertained for each subject and each condition at six representative electrodes (O1 and O2 for occipital cortex, P3 and P4 for parietal cortex, and PO7 and PO8 for parieto-occipital cortex).

Peak Amplitudes

P100 Amplitude

We submitted subjects' P100 amplitude values to a 4-way repeated-measures ANOVA with the factors *group* (young / old), *condition* (RC / IC / NS), *electrode position* (occipital / parietal / parieto-occipital), and electrode *side* (left / right).

Results yielded a significant main effect for *side* (F=4.261; p=0.047), with higher amplitudes at left-sided (O1/P3/PO7) than at right-sided (O2/P4/PO8) electrodes. While we found no significant main effects for *group, condition,* or *position*, we observed a significant interaction *condition x position* (F=2.711; p=0.049), in a sense that amplitude differences between conditions occurred at occipital (O1 and O2) but not other electrodes. A further interaction *condition x position x side* (F=2.856; p=0.041) shows that these differences between conditions were more pronounced over the left hemisphere. We finally found an interaction *condition x position x side x group* (F=2.783; p=0.045) that we cannot account for.

To gain a better understanding of differential reactions between IC, RC, and NS, we performed post-hoc pair-wise t-Tests for young and old subjects separately. The results are displayed in Table 4. We generally found that young subjects' amplitudes for RC were lower than for IC or NS, while the opposite was the case in older observers (higher amplitudes for RC than IC or NS, although differences just failed to reach significance level in most cases). In both groups, no significant disparities in peak amplitude could be evidenced between IC and NS.

	P100 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.001*** IC>RC	p=0.002*** NS>RC	p=0.096	O2	p=0.048* IC>RC	p=0.105	p=0.541
	P3	p=0.172	p=0.138	p=0.702	P4	p=0.097	p=0.058	p=0.896
	PO7	p=0.060	p=0.014* NS>RC	p=0.859	PO8	p=0.825	p=0.369	p=0.857
Old	O1	p=0.443	p=0.025* RC>NS	p=0.205	O2	p=0.391	p=0.941	p=0.106
	P3	p=0.178	p=0.421	p=0.368	P4	p=0.717	p=0.592	p=0.168
	PO7	p=0.312	p=0.319	p=0.612	PO8	p=0.889	p=0.831	p=0.101

Table 4: Post-hoc paired t-Tests for P100 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown.

N150 Amplitude

For the amplitude of the N150 we applied the same 4-way ANOVA as above and found a significant main effect for *electrode position* (F=16.052; p=0.000), indicating higher

amplitudes at occipital than parietal or parieto-occipital electrodes. We also found an *electrode-position* x *side* interaction (F=5.551; p=0.009), in a sense that peak amplitudes at parieto-occipital electrodes were considerably lower in the right hemisphere than the left, which was not the case for parietal or occipital electrodes. Finally, a *group* x *condition* interaction (F=6.721; p=0.004) indicated that younger subjects' peak amplitudes for RC were lower than for IC or NS, but that the opposite (RC > IC/NS) was the case in the older subjects. As for the P100, we performed post-hoc pair-wise t-Tests between conditions for both groups (young / old) separately (see Table 5).

As for the P100, we found that peak amplitudes for RC were generally lower than for IC or NS in the younger group, while in older subjects, RC tended to evoke higher amplitudes than IC or NS. In both groups, however, we could not find significant differential reactions between IC and NS at any of the electrodes.

	N150 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.348	p=0.241	p=0.269	O2	p=0.423	p=0.340	p=0.354
	P3	p=0.060	p=0.048* NS>RC	p=0.732	P4	p=0.021* IC>RC	p=0.038* NS>RC	p=0.504
	PO7	p=0.041* IC>RC	p=0.040* NS>RC	p=0.835	PO8	p=0.783	p=0.237	p=0.426
Old	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.062	O2	p=0.010* RC>IC	p=0.014* RC>NS	p=0.879
	P3	p=0.001*** RC>IC	p=0.001*** RC>NS	p=0.281	P4	p=0.014* RC>IC	p=0.009** RC>NS	p=0.517
	PO7	p=0.003*** RC>IC	p=0.000*** RC>NS	p=0.129	PO8	p=0.151	p=0.525	p=0.759

Table 5: Post-hoc paired t-Tests for N150 peak amplitude between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005). Note that the negative polarity of this ERP component has been taken into account (NS > RC would for example mean that NS had a higher negative amplitude than RC).

P200 Amplitude

A 4-way repeated measures ANOVA of the P200 amplitude revealed a significant main effect for *condition* (F=11.613; p=0.000; amplitudes for RC being higher than for IC or NS), for *electrode position* (F=16.077; p=0.000; higher amplitudes at occipital than parietal or parieto-occipital electrodes), and for *side* (F=18.731; p=0.000; left-hemispheric amplitudes being higher than right-hemispheric ones). There was no significant main effect for *group*.

We furthermore found significant 2-way interactions for *group* x *position* (F=4.928; p=0.014; young subjects tended to have higher amplitudes at parietal electrodes while older subjects had higher amplitudes at parieto-occipital electrodes), for *position* x *side* (F=7.820; p=0.003; indicating larger side differences between occipital and parieto-occipital than parietal

electrodes), and for *condition* x *position* (F=3.4.4; p=0.021; indicating larger amplitude differences between conditions at occipital than parieto-occipital or parietal electrodes).

A significant 3-way interaction *condition* x *position* x *side* (F=7.748; p=0.000) signified that differences between conditions were more pronounced in the left hemisphere, particularly at occipital electrodes. Finally, a significant 3-way interaction *position* x *side* x *group* (F=3.519; p=0.042), showed that the side differences were more distinct in the older group, especially at occipital electrodes.

Here, too, we performed post-hoc pair-wise t-Tests between conditions for both groups (young / old). In young subjects, we found that peak amplitudes for RC were larger than for IC and NS at most of the investigated electrodes (see Table 6). Unlike in the previous conditions we observed a significant differential reaction between IC and NS at electrode P4 (right parietal).

In the older subjects, amplitudes for RC were higher than for IC and NS at most electrodes (see table 6). While we could not evidence significant differences between IC and NS in this group, disparities in peak amplitude approached significance level at several electrodes (O1 (T=1.861; p=0.077), P3 (T=1.839; p=0.080), P4 (T=2.060; p=0.052), PO7 (T=1.953; p=0.065)). As in the young subjects, amplitudes for NS tended to be larger than for IC in this particular comparison.

	P200 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.001*** RC>IC	p=0.001*** RC>NS	p=0.139	O2	p=0.038* RC>IC	p=0.017* RC>NS	p=0.169
	P3	p=0.004*** RC>IC	p=0.074	p=0.814	P4	p=0.016* RC>IC	p=0.076	p=0.008** NS>IC
	PO7	p=0.003*** RC>IC	p=0.009** RC>NS	p=0.335	PO8	p=0.229	p=0.491	p=0.266
Old	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.077	O2	p=0.021* RC>IC	p=0.017* RC>NS	p=0.268
	P3	p=0.060	p=0.238	p=0.080	P4	p=0.000*** RC>IC	p=0.113	p=0.052
	PO7	p=0.020* RC>IC	p=0.117	p=0.065	PO8	p=0.269	p=0.205	p=0.834

Table 6: Post-hoc paired t-Tests for P200 peak amplitude between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

Peak Latencies

P100 Latency

Similar to amplitudes, latency values of the P100 were submitted to a 4-way repeated-measures ANOVA with the factors *group* (young / old), *condition* (RC / IC / NS), *electrode position* (occipital / parietal / parieto-occipital), and electrode *side* (left / right). We found significant main effects for *condition* (F=3.602, p=0.039, RC peaking earlier than IC or NS)

and *electrode position* (F=10.788, p=0.000, earlier peaks at occipital than at parietal or parieto-occipital electrodes). A main effect for group just missed significance (F=3.516; p=0.070); most interestingly it was the group of older subjects who tended to have shorter P100 latencies. Furthermore, we found a significant interaction *condition* x *side* x *group* (F=5.574; p=0.009), in a sense that the peak for RC occurred generally earlier than for IC and NS, with the exception of the right-sided electrodes in young subjects (later peak for RC than for any other condition).

As for peak amplitudes, we performed post-hoc paired t-Tests to pinpoint the exact nature of the observed condition effect (see Table 7). We found that the condition effect was mostly the result of prolonged latencies of NS and IC as compared to RC in the overall data (with exception of right-sided electrodes in young subjects, see above), but not of differences between IC and NS.

	P100 Peak Latency – Post-hoc Comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.120	p=0.021* RC→NS	p=1.000	O2	p=0.301	p=0.042* NS→RC	p=0.318
	P3	p=0.423	p=0.038* RC→NS	p=0.552	P4	p=0.216	p=0.026* NS→RC	p=0.338
	PO7	p=0.017* RC→IC	p=0.017* RC→NS	p=0.624	PO8	p=0.304	p=0.417	p=0.198
Old	O1	p=0.159	p=0.089	p=0.201	O2	p=0.387	p=0.063	p=0.263
	P3	p=0.086	p=0.355	p=0.127	P4	p=0.178	p=0.071	p=0.813
	PO7	p=0.093	p=0.561	p=0.144	PO8	p=0.267	p=0.238	p=0.909

Table 7: Post-hoc paired t-Tests for P100 peak latency between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown (RC→IC for example means that for RC the peak occurs earlier than for IC).

N150 latency

For the latency of the N150, our analyses (same as above) revealed a significant main effect for *condition* (F=16.602; p=0.000; RC peaking earlier than IC or NS), for *electrode-position* (F=21.728; p=0.000; earlier peaks at occipital than at parietal or parieto-occipital sites), and for *side* (F=7.349; p=0.010; earlier peaks at left-sided electrodes). We furthermore found a significant interaction *position x side* (F=3.933; p=0.030) which indicated that left-right-differences were more pronounced at parieto-occipital than at other electrodes.

Our post-hoc t-tests on the N150 confirmed that the observed condition effect was the result of prolonged latencies of IC and NS as compared to RC, but that NS and IC could not be distinguished in term of peak latency.

	N150 Peak Latencies – Post-hoc Comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.011* RC→IC	p=0.036* RC→NS	p=0.638	O2	p=0.214	p=0.025* RC→NS	p=0.833
	P3	p=0.000*** RC→IC	p=0.052	p=0.204	P4	p=0.001** RC→IC	p=0.027* RC→NS	p=0.862
	PO7	p=0.000*** RC→IC	p=0.004** RC→NS	p=0.351	PO8	p=0.748	p=0.248	p=0.346
Old	O1	p=0.083	p=0.028* RC→NS	p=0.534	O2	p=0.152	p=0.169	p=0.565
	P3	p=0.004** RC→IC	p=0.008** RC→NS	p=0.882	P4	p=0.000*** RC→IC	p=0.071	p=0.285
	PO7	p=0.012* RC→IC	p=0.034* RC→NS	p=0.221	PO8	p=0.125	p=0.137	p=0.701

Table 8: Post-hoc paired t-Tests for N150 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

P200 latency

For the latency of the P200 component, our analyses revealed a significant main effect for *electrode position* (F=4.515; p=9.019; earlier peaks at occipital than at parietal or parieto-occipital sites), for *side* (F=6.192; p=0.018; earlier peaks in the left than in the right hemisphere), and for *group* (F=4.724; p=0.037; earlier peaks in young subjects). We also found an interaction *side x group* (F=4.624; p=0.039) which indicated that young subjects' peaks always occurred first in the left hemisphere, while partially the opposite was the case in older subjects. A further interaction *condition x side* (F=3.587; p=0.040) revealed that peaks for RC arrived earliest in both hemispheres, but that NS had shorter latencies compared to IC in the left hemisphere, while peaks for IC preceded those for NS in the right hemisphere. We found, however, that this pattern was not the same in young and old subjects, as was indicated by an interaction *condition x side x group* (F=3.933; p=0.030): while young and old subjects reacted relatively similar in the left hemisphere (shortest latencies for RC, than NS, than IC), young subjects latencies for RC tended to be longer in the right hemisphere compared to IC and NS (which did not differ among themselves). Older subjects, however, had the longest latencies in the right hemisphere for NS, followed by IC, and shortest latencies for RC.

	P200 peak latencies – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.911	p=0.622	p=0.323	O2	p=0.257	p=0.829	p=0.209
	P3	p=0.498	p=0.492	p=0.891	P4	p=0.277	p=0.223	p=0.665
	PO7	p=0.147	p=0.847	p=0.171	PO8	p=0.783	p=0.935	p=0.508
Old	O1	p=0.931	p=0.777	p=0.730	O2	p=0.440	p=0.106	p=0.468
	P3	p=0.041* RC>IC	p=0.029* RC>NS	p=0.631	P4	p=0.277	p=0.001** RC>NS	p=0.031* IC>NS
	PO7	p=0.049* RC>IC	p=0.107	p=0.675	PO8	p=0.126	p=0.004** RC>NS	p=0.250

Table 9: Post-hoc paired t-Tests for P200 peak amplitude between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

3.2.4. Discussion

Certainly, the most interesting aspect about our results consists in the very weak IC effect we found both in young and older observers. We found the typical VEP components in all three stimulus conditions, but while the electrophysiological response to RCs clearly differed from the other two conditions, little to no differences could be found between ICs and NCs. Previous investigations (with EEG and MEG methods) consistently reported a differential reaction between ICs and NSs around 150 ms post-stimulus (Kruggel et al, 2001; Herrmann & Bosch 2001; Murray et al. 2002; Murray et al. 2004; Halgren et al. 2003; Korshunova 1999); this was not the case here. Neither were there remarkable differences in GFP as reported in other studies (Murray et al. 2004; Pegna et al. 2002). Our results of the map series analysis, that the different shapes are processed within the same brain areas (indicated by identical cortical maps), go hand in hand with previous investigations (Murray et al. 2004; Pegna et al. 2002). Finally, the analysis of peak amplitudes and latencies failed to reveal significant differences between ICs and NSs, except for young subjects' P200 amplitude at the right parietal electrode P4. In contrast, most of our analyses put forward clear differences between RCs and the other stimulus conditions, with shorter latencies but lower amplitudes for RCs, as has been reported previously (Pegna et al., 2002). Since our RC stimuli in this experiment differ in overall luminance from the IC- and NS-stimuli, though, we will not discuss those differential reactions further.

What could be the reason for this almost non-existent IC-effect? Did subjects actually perceive the ICs in this experiment? For the latter question we have no answer, because no response whatsoever was demanded from the subjects in this experiment. On the other hand, the complete perception of the illusory form, including the sensation of enhanced

brightness, would probably have been accompanied by modulations in the electrophysiological signal, distinguishing the IC stimuli from the NSs. One may almost have the impression that the brain did not “bother” to build out the percept of an illusory form (as our instruction only demanded the fixation of the central cross). While most studies published on EEG responses to ICs used experimental setups in which subjects had to respond to different types of stimuli (mostly by pressing corresponding buttons), Korshunova (1999) also applied a passive paradigm. They, however, reported a differential reaction between IC stimuli and NSs around the N150 and later VEP components, which we could not confirm here. What else could therefore explain our findings? With a distance of 6° of visual angle between inducer centres, the stimuli we had used were somewhat larger than in most other studies (> 5° in most cases); although psychophysical experiments have proven that ICs can easily built up between distances up to 13° (Ringach & Shapley, 1996), stimulus size might, however, have played a role here: considering that subjects’ attentional focus was directed to the small fixation cross in the screen centre, it might be harder to achieve a visual binding of elements at higher eccentricities – in case IC formation is not an entirely automatic process after all.

3.2.5. Conclusion

The absence of an IC effect in both young and older subjects in this experiment raises a number of questions. Was the stimulus material we used inadequate (i.e., too large) to produce a distinct IC effect? Or is attention a more vital factor in IC perception as is commonly thought? Would the results be different if the stimuli were processed more consciously?

To find out whether stimulus size was the main reason for the weak IC effect, we designed Experiment 4.a), which is identical in procedure with the present experiment, but with reduced stimulus size. As a second step, we developed Experiment 4.b), in which we test whether (object-based) attention modulates the electrophysiological responses associated with shape processing; stimulus size will be held constant (compared to Experiment 4.a), but new target stimuli will be introduced to direct subjects’ attention to the presented shapes.

3.3. Experiment 3 – The effect of stimulus size in IC perception (psychophysics)

3.3.1. Subjects

Two groups of subjects, twenty young and twenty elderly observers took part in this experiment. Young subjects' age ranged from 20 to 35 years, elderly subjects were aged between 65 and 86 years (see table 10 for details).

Subjects were recruited via message boards at the University of Göttingen, among participants of the University of the Third Age, and in local sports clubs. They received 15€ for participation.

All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971).

Group	***n***	***Age (sd)***	***Gender***
1: 20-35 years	20	24.8 *(4)*	8m, 12f
2: 57-82 years	20	70.3 *(6)*	8m, 12f

Table 10: Demographic data of participants in Experiment 3

Inclusion / exclusion criteria

The same inclusion and exclusion criteria (concerning visual parameters, medication, cognitive status, and education) as in the two previous experiments were applied. Elderly participants passed a German version of the neuropsychological test battery that was described in Experiment 1.

Prior to participation all participants were informed about the purpose of the study gave their written consent.

3.3.2. Stimuli and procedure

The experiment consisted of two parts, one of which was identical to Experiment 1 (see Chapter 3.1). The other part was identical in procedure, but stimuli only had half the size (the side length of a real or illusory triangle would though correspond to 5° of visual angle); length proportions would however remain the same as in Experiment 1.

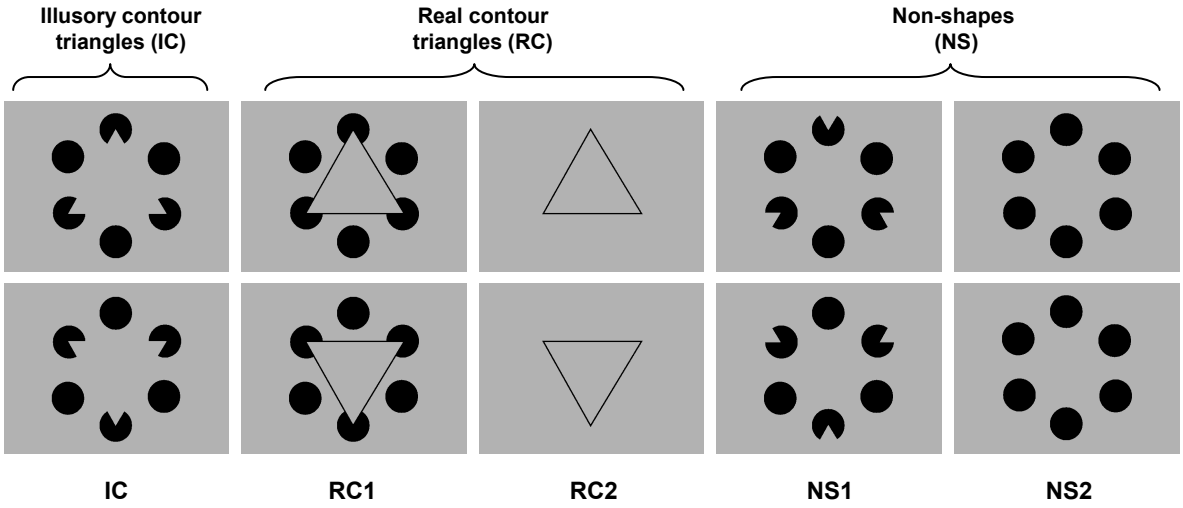

Fig. 15 : Perception of illusory contours ; psychophysical experiment : stimuli

As in Experiment 1, subjects received instructions to press one marked button of the keyboard if they perceived a triangle (real or illusory) in the display, and another one if they did not. They also passed a training phase (with unlimited viewing duration) until instructions seemed well understood.

Half of the subjects in each group (the young and the older subject group) started with the smaller set of stimuli, the other half with the bigger set of stimuli. Before the second part started, participants were informed that stimuli would now be bigger, respectively smaller, than in the previous part, but that their task would remain the same.

Data processing

Median response times (restricted to valid trials only) and percentage of errors per stimulus condition were calculated for each participant for each part (big / small stimulus set). To separate stimulus-specific slowing effects from general slowing, we furthermore introduced an additional experiment to assess individual simple reaction times (this experiment is described below). Median response times for each condition were then normalised to this value (as 100%).

Statistical analysis was based on a 2 (age group) x 5 (condition) x 2 (big / small stimulus set) repeated measures ANOVA. Separate analyses were performed on normalized reaction times and error rates.

Additional Experiment: simple reaction times

As our two-choice decision tasks (triangle / no triangle) yield no direct information whether a delay of response time in the older group is an effect of generally slowed reaction times, or rather represent a slowing in the categorisation of the stimulus, we decided to introduce another experiment. That very simple reaction time task should give an individual baseline reaction time value (for responding to the presence of a simple visual stimulus) that would then be used for normalizing the results of the psychophysical IC-experiments.

The experiment was programmed by Dipl.Ing. Torsten Wüstenberg (University of Göttingen) with Presentation (© Neurobehavioral Systems, USA; version 071092403).

In the actual task, participants were to react as quickly as possible to a simple visual stimulus appearing in the centre of a 15'' computer screen. The stimulus consisted of a 4 x 4 cm black "X", presented on grey background, viewed at a distance of 40 cm (corresponding to a visual angle of 5.7°).

To start a trial, subjects were asked to press a start-button (the Alt Gr-key on the keyboard) with their right index finger. They were instructed to hold that button down until they saw the target, a black X, appearing on the otherwise empty screen. In that case they were to release the button immediately and press the neighbouring space bar (with the same finger) as quickly as possible. If the start-button was released before the target appeared on the screen, the trial counted as invalid.

Time between pressing of the button and the appearance of the stimulus varied between 1200 and 2200 ms (in ten 100ms steps); the different intervals were presented in randomized order. Once subjects had responded to the target, they could set off the next trial by pressing the start-button anew. The participants were thereby allowed to set their own pace in this task.

A total of 110 stimuli were presented; the first ten trials were considered as practice trials and were discarded from further analyses.

The method of using a go- and response button provides a measure of the central cognitive aspect (release time of the go-button), movement time (time between release of go-button and pressing of response button), and total reaction time (Pöppel et al. 1990).

As our primary interest consisted however in determining a baseline value for normalizing the response times of the IC-experiments, we did not perform detailed analyses on these data.

We chose the individual median values of the release times to normalize the response times of the different conditions in the IC experiments upon.

3.3.3. Results

The results of Experiment 3 (before normalization) are displayed in Figure 16:

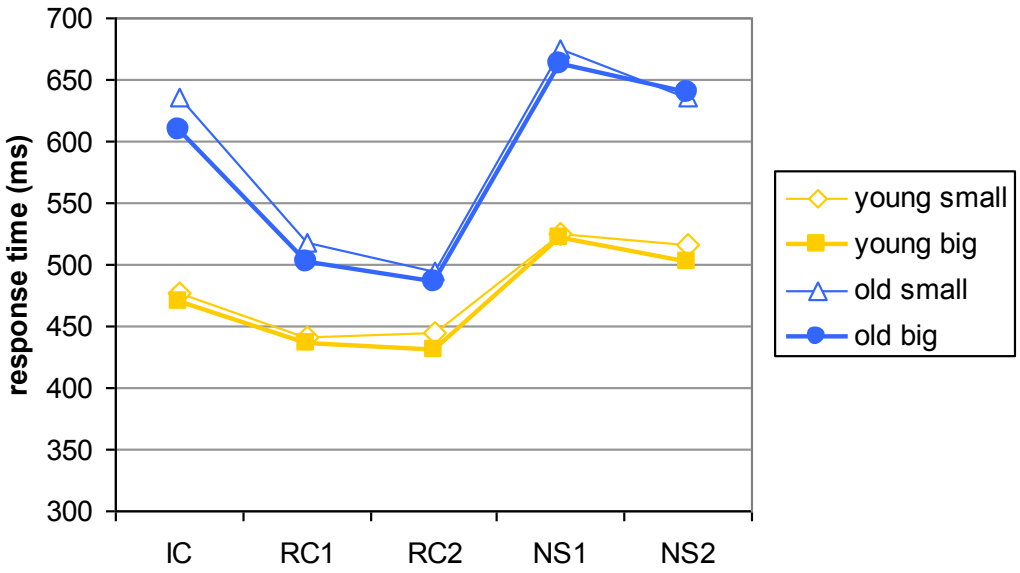

Figure 16: Mean response times per age group and condition, for big and small stimuli

	IC *Mean* *sd*	***RC1*** *Mean* *Sd*	***RC2*** *Mean* *sd*	***NS1*** *Mean* *sd*	***NS2*** *Mean* *sd*	***All conditions***
Young, small stimuli	477.55 *77.7*	441.35 *77.2*	444.73 *75.6*	524.35 *88.5*	515.28 *97*	480.65 38.6
Young, big stimuli	470.38 *78.8*	436.2 *82.6*	430.38 *66.8*	521.0 *108.3*	502 *91.8*	472.0 39.7
Old, small stimuli	635.17 *113.3*	517.9 *95.1*	495.38 *70.3*	674.35 *92.5*	635.5 *78.4*	591.66 79.6
Old, big stimuli	609.48 *90.7*	502.13 *84.5*	486.13 *77.6*	661.65 *122.3*	639.05 *120.8*	579.69 80.5

Table 11: Average median response times (ms) per group and condition

As can be seen in Figure 16 and Table 11, differences in response times between the larger and the smaller stimulus set were marginal, in both the older and the younger subject group. Repeated measures ANOVA (size × condition × group), revealed a significant condition effect ($F_{4,35}$= 48.24; p<0.001) and group effect ($F_{1,38}$=20.77; p<0.001), and a group × condition interaction (F4.35= 10.66; p<0.001). This confirmed the results from Experiment 1. No main effect was observed for stimulus size, or any interaction of size with group or condition.

We furthermore tested whether the series, in which subjects solved the task, starting with either the small or the big stimulus set, would influence test performance. One-way ANOVA (order of administration) which was performed separately for the small and big stimuli revealed, however, no significant effects for this factor. The order of solving the task thus plays no role.

We could furthermore not evidence significant training effects in this task. Response times in the second experiment in both groups (irrespective of the stimulus size) were not significantly shorter than in the first of the two experiments.

Supplementary Experiment: Simple Reaction Times

A supplementary experiment on simple reaction times was mainly performed to obtain a baseline for normalizing response times of the two Kanizsa experiments. Results will be described only briefly below.

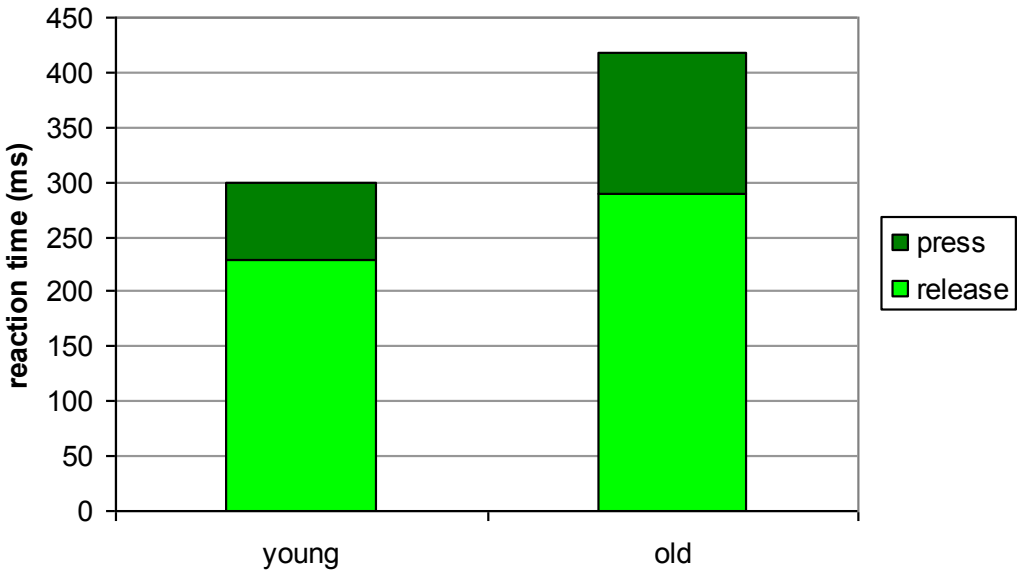

Figure 17: Mean reaction times (composed of press and release time) per age group

Figure 17 depicts the composite reaction times (time for releasing the go-button, plus pressing the response button) for the young and old participants. One-way ANOVA (group) revealed that older subjects released the go-button significantly later than the young participants ($F_{1,38}$=18.22; p<0.001), and needed more time to press the neighbouring response button ($F_{1,38}$=8.77; p=0.005), leading to a significant group effect in the total reaction time ($F_{1,38}$=11.29; p=0.002).

For each subject, we then took the individual reaction time and normalized their response times for the various conditions from the two Kanizsa experiments by that value (for example [(response time IC / simple reaction time) * 100] etc.).

Figure 18 depicts group averages for the various conditions after normalization:

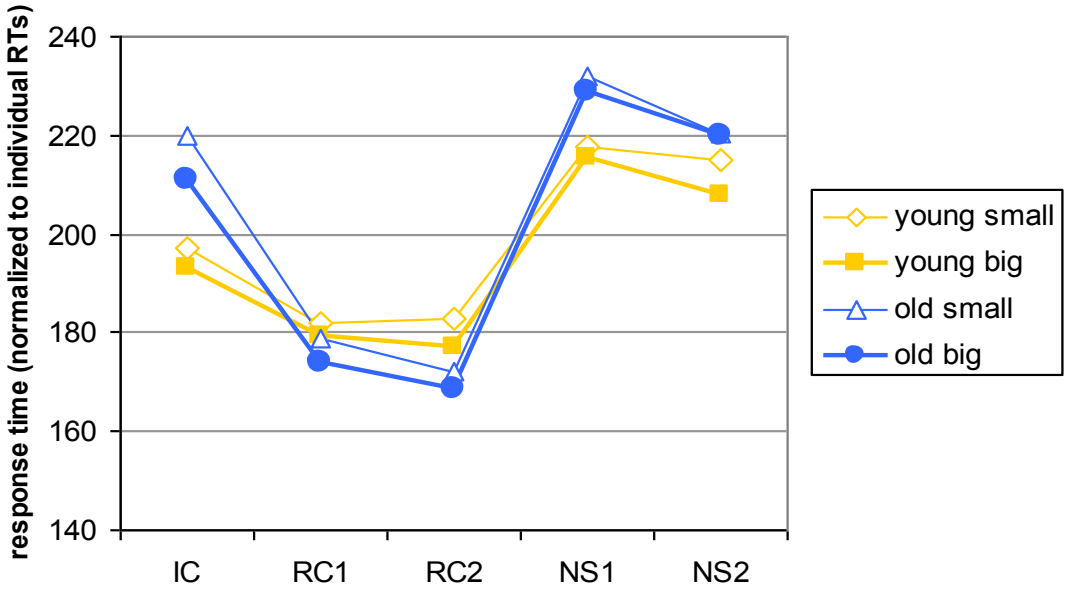

Figure 18: normalized response times for big and small stimuli

As can be seen in Figure 18, older individuals do not necessarily require more proportional time to reach a decision (in case of the real contour triangles), than do young subjects. They seem, however, more hesitant when it comes to the IC or the target-absent conditions (NS1 and NS2). We performed repeated measures ANOVA (size × condition × group) on these data and once again found a significant condition effect ($F_{4,35}$= 52.09; p<0.001) and a significant group × condition interaction ($F_{4,35}$= 8.13; p<0.001). There was no significant main effect for group but a tendency for a main effect of stimulus size ($F_{1,38}$= 2.89; p=0.097). It should, however, be noted that this effect was not taking the expected direction, i.e., subjects did not profit from the decreased stimulus size (to make binding easier), but responded rather more quickly to the larger stimuli. No other effect or interaction reached significance level.

c) Error Rates

Young and older participants' error rates (%) for both the big and the small stimuli are displayed in Figure 19:

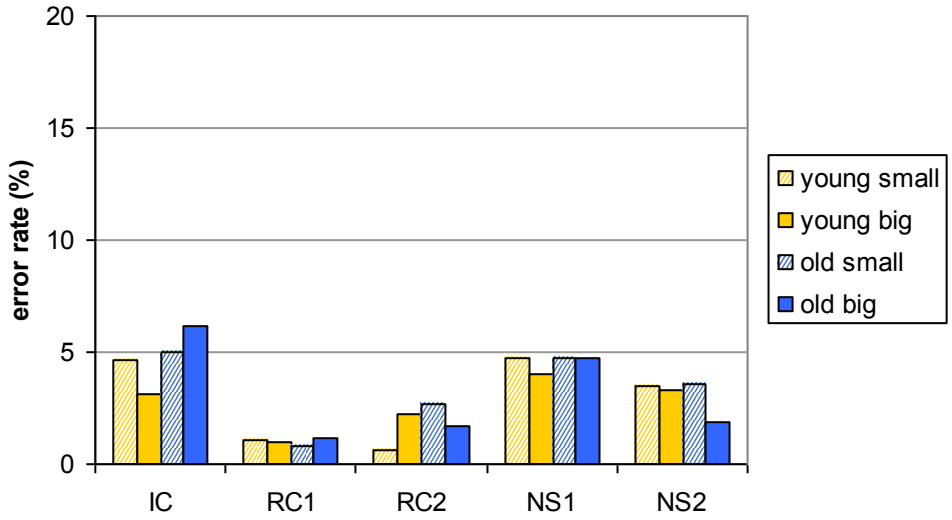

Figure 19: Error rates (%) for the large and small stimulus set in young and old observers for the five stimulus conditions

Similar to Experiment 1, subjects made very few errors in this task, in most cases below 5%. We performed repeated measures ANOVA (size × condition × group) on the data. Results revealed a significant condition effect ($F_{4,35}$= 8.422; p<0.001) but no other main effects or interactions. As for the response time data, the role of stimulus size seems negligible.

Repeated measures ANOVA (order of administration × group), which was performed on the total error rates (of all 5 stimulus conditions), furthermore revealed that error rates were relatively stable, i.e., subjects did not make significantly less errors in the second trial (irrespective of stimulus size).

3.3.4. Discussion

These results largely replicate our findings from Experiment 1, suggesting generally a very robust effect. Response times and error rates were similar in the first and second trial, so performance was not significantly improved by practice.

We had then normalized the data to simple reaction times to get an impression which proportion of the response times reflects the general process of decision making and which part is stimulus specific. Our data revealed that older adults did not generally need more time for the decision process (see Figure 18), but only in the case of illusory contours or target absence. Slower response times in older observers in target-absent conditions have been reported previously (see for example Levinoff et al. 2002) and will not be discussed here. The prominent increase in response time for illusory contours for the older subjects is of interest, however: it might stem from a deficit or delay of the perceptual processing of IC in older observers, which might alter or retard the subjective percept of IC (e.g., brightness,

pop-out), requiring compensatory (and time-demanding) cognitive strategies to arrive at the correct answer.

Finally, we had wanted to assure that our observations from Experiment 1 were not the result of an inappropriate stimulus design, disadvantaging older observers (with respect to the reduction of the UFOV; see the discussion of Experiment 1). Our data revealed, however, that decreasing the stimulus size did not facilitate the task for any of the groups; on the contrary, both groups performed by trend somewhat quicker when the large stimulus set was presented.

3.4. Experiment 4 – The perception of illusory contours in young and older observers – passive vs. active viewing (EEG)

3.4.1. Experiment 4.a – passive viewing

3.4.1.1. Subjects

Subjects for this EEG-experiment were recruited among the participants who had participated in Experiment 3, so the same inclusion / exclusion criteria applied here. Three of the elderly subjects were not available for the EEG recording, so the group of elderly subjects only comprised 17 participants (see Table 12 for demographic data).

	n	***Age range***	***Age (sd)***	***Gender***
Young subjects	20	20-35	24.8 *(4)*	8m, 12f
Elderly subjects	17	65-86	70.3 *(6)*	7m, 10f

Table 12: Demographic data of participants in Experiment 4

3.4.1.2. Stimuli and procedure

Stimuli presented in this paradigm were similar to those used in EEG Experiment 2: RC, IC, and NS images (see Fig. 20). As in the previous EEG experiment, shapes were black (0.36 cd/m^2) on grey (75 cd/m^2) background and were presented on a 17'' LCD screen placed at 1.60 m distance from the observer.

To find out whether the poor IC-effect observed in Experiment 2 was related to the relatively large stimuli that were used (>7° of visual angle), we now presented smaller stimuli: the side length of a real or illusory triangle was 4° of visual angle, and the diameter of the inducer clipped circles about 1.25° (corresponding to a support ratio of approximately 0.31). The line thickness of the real contour triangle was 0.056°. As in the previous EEG experiment, a fixation cross (around 0.23° of visual angle in diameter) was placed in the middle of the screen, remaining there throughout the experiment.

The experiment was programmed with the public domain version of Presentation (© Neurobehavioral Systems, USA; version 0.71) by Dipl. Ing. Torsten Wuestenberg (University of Göttingen).

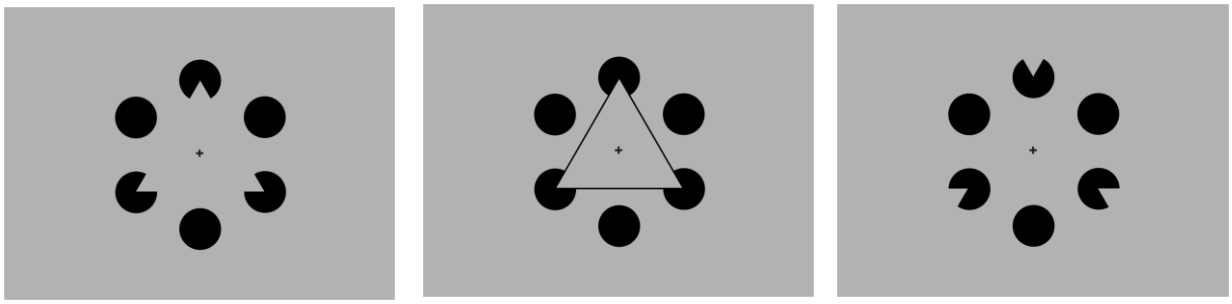

Figure 20: Stimuli used in experiment 4.a)

As in Experiment 2, the first part of this task was a non-response paradigm. Subjects were seated in a comfortable chair and were asked to focus the fixation cross and, if possible, avoid any movement. The experiment was performed in an electrically shielded, sound-attenuated room.

Stimuli were presented for 500 ms, followed by a blank screen with only the fixation cross. Time between two successive presentations was 1100 ± 100 milliseconds, randomly jittered in 10-ms intervals. Stimuli were presented in pseudo-randomized order; each of the three stimulus types at least 150 times. To not overstrain subjects' eyes, the recording was subdivided into six blocks, the duration of each not exceeding 2 minutes.

Recording parameters

Continuous 64-channel EEG was acquired by a BrainAmp (© Brain Products GmbH; Munich, Germany) recording system, using sintered Ag/AgCl ring electrodes mounted in an elastic cap (Easy-Cap; Falk Minow Services; Herrsching-Breitbrunn, Germany) according to the extended 10-10 system (Fig. 21). The sampling rate was 5000 Hz. Ground electrodes were placed at the left and right mastoid (TP9/TP10) and all electrodes were referenced to the vertex (FCz). Electrode impedance was kept below 5 kΩ. Eye movements were monitored with additional electrodes placed at the outer canthi of the eyes and inferior orbits. Electrophysiological signals were amplified and analog-filtered online using a 0.5–70 Hz band pass. Amplifier settings were 0.5 µV resolution; range: + 16.384 µV; low cutoff: 10 s; high cutoff 250 Hz.

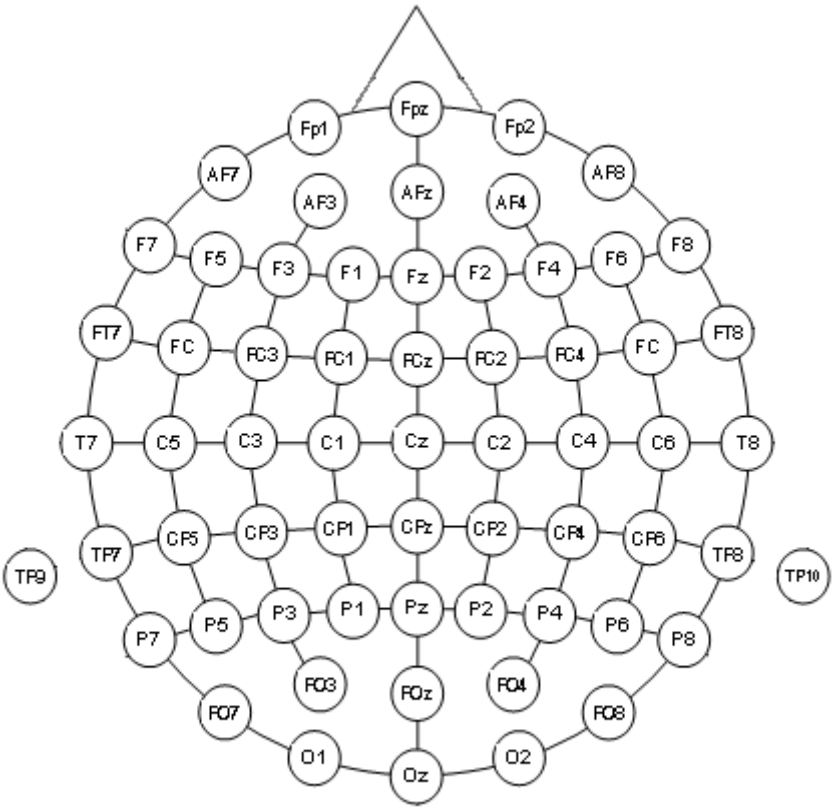

Figure 21: Montage of 64-channel EEG recording system

3.4.2. Experiment 4.b – active viewing

The question underlying Experiment 4.b was whether a more conscious processing of the stimuli – induced by a special instruction – would lead to enhanced VEP differences between stimuli.

3.4.2.1. Subjects

Experiment 4.b was performed within the same recording session as Experiment 4.a, so see the corresponding section above for demographic details of participants.

3.4.2.2. Stimuli and procedure

Most of stimuli presented in this experiment were identical to those used in EEG experiment 4.a. We now introduced new (rare) target stimuli, however: one curved RC and one curved IC figure (Fig. 22).

The two curved figures were the target stimuli and subjects were instructed to silently count their occurrence (with either real or illusory outlines) within a recording block. Similar paradigms were used by Tallon-Baudry and collaborators (for example Tallon et al. 1995; Tallon-Baudry et al. 1997). The curved triangles were presented as both RC and IC versions

to avoid possible attentional biases towards the presence or absence of “real” (physical) contours.

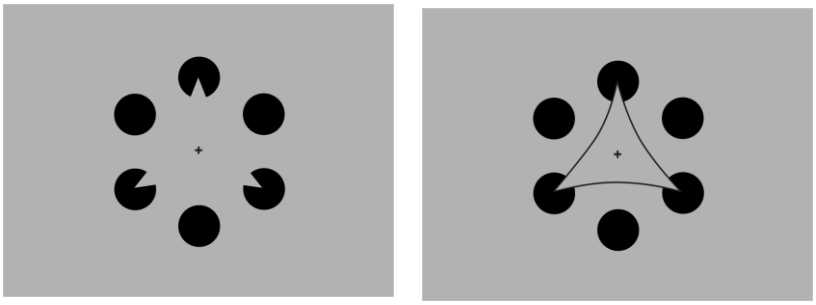

Figure 22: Target stimuli in Experiment 4.b)

Target stimuli had the same colour and size as the “normal” stimuli. They would occur randomly, between two and ten times within each recording block. One recording block therefore comprised 25 IC, 25 RC, and 25 NS stimuli, presented in pseudo-randomized order (identical to Experiment 4.a), plus the curved RC and IC target stimuli (at least one and at most five of each kind).

As in the previous experiment, stimuli were presented for 500 ms, followed by a blank screen except for the fixation cross; the time between two successive presentations was 1100 $\pm$ 100 milliseconds, randomly jittered in 10 ms intervals. Six recording blocks were passed.

The experiment was performed subsequent to Experiment 4.a). Subjects were instructed that they now had to perform a task. The target figures, the curved IC and RC, were shown as print-outs to the subjects. They were informed that these figures would now appear randomly among the figures they had seen in the previous experiment, and that they were to count the curved triangles they detected within a trial. After each trial, the experimenter would enter the recording chamber and note subjects’ answers.

Recording parameters

Since both experiments 4.a) and 4.b) were conducted within the same session, see above for recording parameters.

Data processing

Behavioural data:

Subjects’ answers (how many curved triangles they had counted) were compared to the number of target stimuli that were actually shown (as documented in the log-file). Error rates were rather low (<5%) for both young and older participants, so we assume that the instructions were well understood. There was no apparent difference in error rate between

age groups. Since the introduction of targets mainly aimed at directing subjects' attention towards the non-target stimuli, these data were not further processed.

EEG data:
Using the Brain Vision Analyzer Software (Version 1.05.0001; © Brain Products GmbH; Munich, Germany), we computed averages for each subject and each condition (IC/RC/NS), epochs lasting from 100 ms before to 600 ms after stimulus onset. Data of the passive and the active paradigm were processed separately. All epochs were inspected for artefacts and trials containing artefacts (eye movements or electrode drifts) were rejected. Data for target stimuli in Experiment 4.b) were not evaluated, since the number of stimulus presentations was not sufficient to produce a reliable VEP.

To gain a first impression of possible stimulus effects in the different subject groups, we performed t-tests (for dependent samples) for each amplitude at each time frame on the group-averaged VEPs between conditions (i.e., RC vs. IC, RC vs. NS, IC vs. NS; see Fig. 25 and 26). This was done to determine in which temporal windows differential reactions occur, and which electrodes were implicated. Moreover, a t-test for dependent samples was applied for testing the time course of differences in global field power (GFP) between conditions. We used the same programs for the t-tests (for amplitude and GFP) as in Experiment 2.

Two types of analyses were conducted subsequently:
Map series analysis of the VEP: The map series analyses were performed with the same methods as in Experiment 2 (see page 29 and 30). This time, data of young and older observers were processed separately, but data of the passive and the active viewing paradigm were processed together. In a first step, the grand means (mean VEP for young, respectively older subjects) were determined for each condition for the passive and the active paradigm. On the basis of these data, a segmentation of the different spatial configurations (« micro-states ») across time was conducted. Differences in map topography within one paradigm would indicate that different stimulus types would be processed in distinct brain areas, while differences between passive and active viewing within one stimulus-condition would hint at an attention-related additional recruitment of hitherto less active brain areas.

Peak analysis of the VEP: The amplitudes (in µV) and latencies (in ms) of the VEP peaks P100, N150 and P200 for six representative electrodes (O1, O1, P3, P4, PO7, PO8) were determined (by visual inspection) for each subject and each condition in the passive and in the active paradigm. In a second step, amplitudes and latencies of the peaks were tested with a 4-way MANOVA (preceded by descriptive statistics) for *condition* effects (RC/IC/NS),

group effects (young/old), *position* effects (occipital/parietal/parieto-occipital), *side* effects (left/right hemisphere) and possible interactions.

3.4.3. Results

Grand averaged ERP waveforms for the conditions RC (black lines), IC (red lines), and NS (green lines) for eight representative electrodes at different scalp positions (Fp1, Fp3, C3, C4, P3, P4, O1, O2) are displayed in Figure 23 (for young subjects), and 24 (for old subjects). ERPs of Experiment 4.a), in which stimuli were not particularly attended to, are represented by dotted lines, while ERPs from Experiment 4.b), in which stimuli were to be attended (in order to distinguish them from the target) are represented by solid lines. GFP curves for each group are shown below the corresponding figures.

A first visual inspection of these curves reveals that the impact of the instruction (attend stimuli vs. attend fixation point) clearly evokes modulations of the ERP in the magnitude of condition effects (IC/RC/NS), or even larger. Concerning effects of stimulus size, at first glance these data largely resemble our results from Experiment 2, with distinct differences between RCs and ICs/NSs, and less pronounced differences between ICs and NSs (see dotted lines). However, these differences do at first sight not seem to increase with the *attention* condition.

Concerning the GFP curves, attention seems to go along with higher GFP in young observers as compared to passive viewing, while GFP rather decreases in older observers in the *attention* condition. As for the ERPs, the majority of condition and attention effects do not seem to occur sooner than around the N150.

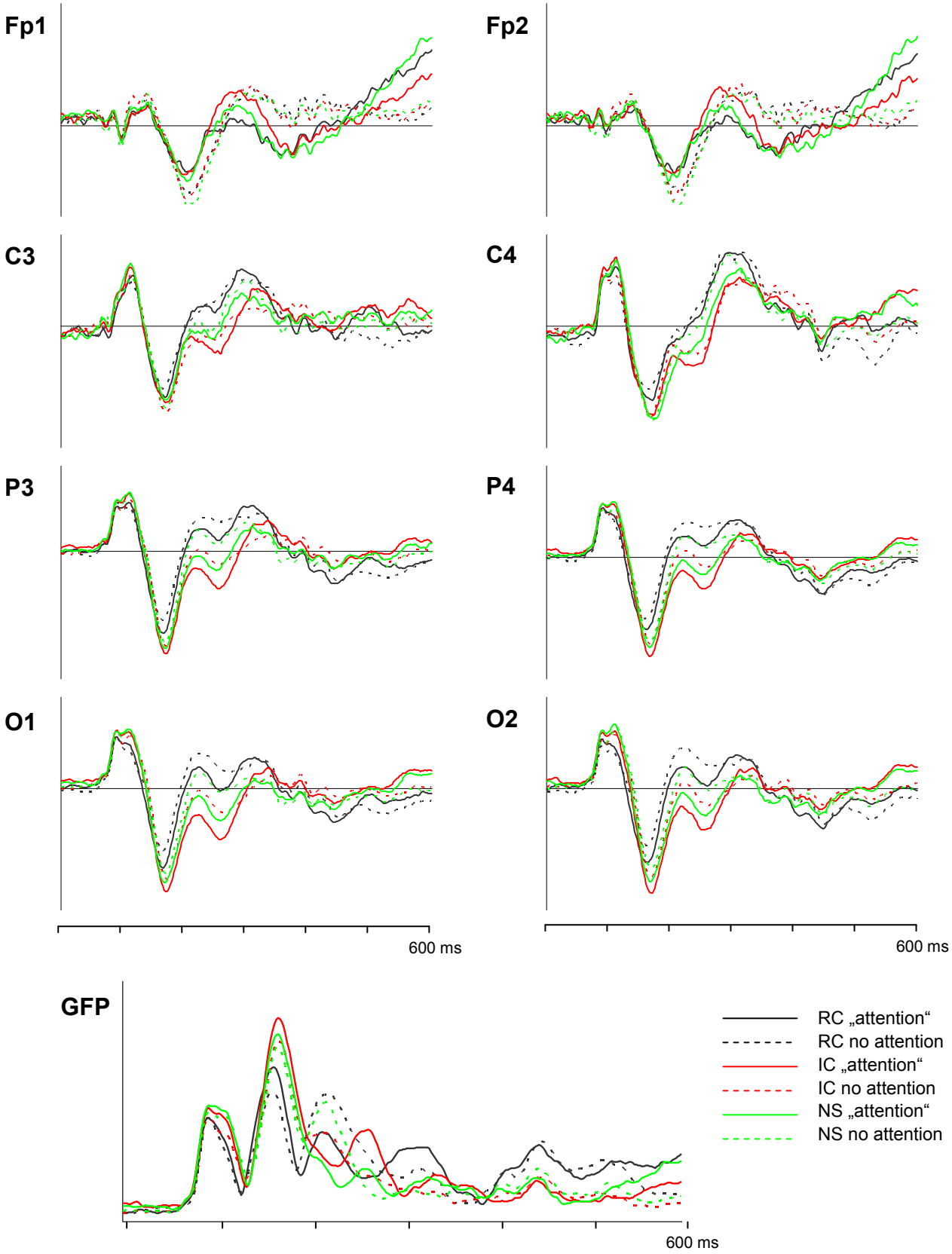

Figure 23: Young subjects; grand average ERP waveforms (positive polarity shown upwards) of eight selected electrodes and GFP curve for the conditions RC, IC, and NS, viewed once in a passive paradigm (“no attention”; Experiment 4.a), and then attentively (“attention”; Experiment 4.b).

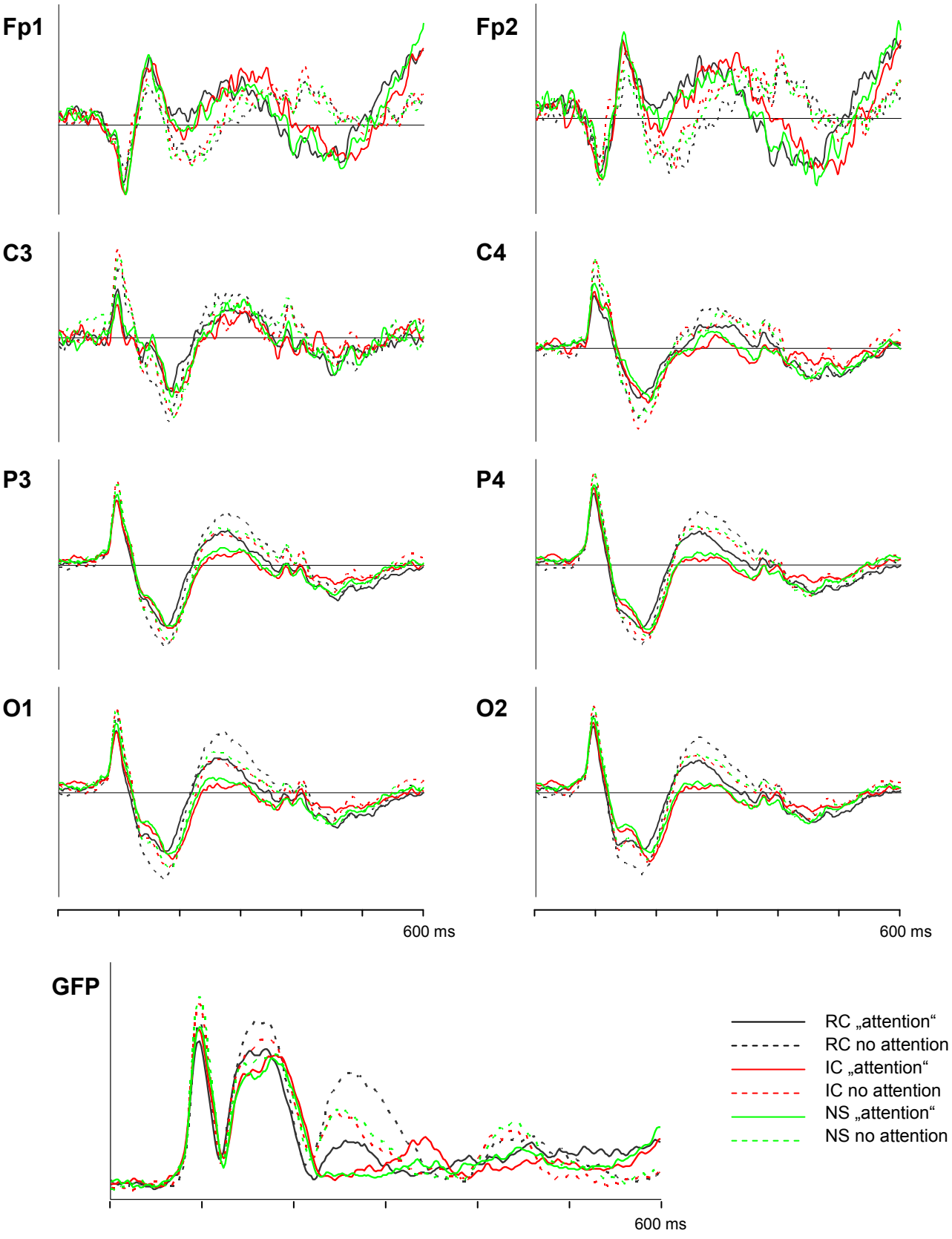

Figure 24: Old subjects; grand average ERP waveforms (positive polarity shown upwards) of eight selected electrodes and GFP curve for the conditions RC, IC, and NS, viewed once in a passive paradigm (“no attention”; Experiment 4.a), and then attentively (“attention”; Experiment 4.b).

T-Test of VEP amplitude over time

As in Experiment 2, we performed pair-wise t-Tests of VEP amplitude between two conditions at a time, to gain a first insight on the time course of (possible) differential reactions. Results of Experiment 4.a) and 4.b) are displayed in Figure 25 for young subjects, and in Figure 26 for the older participants.

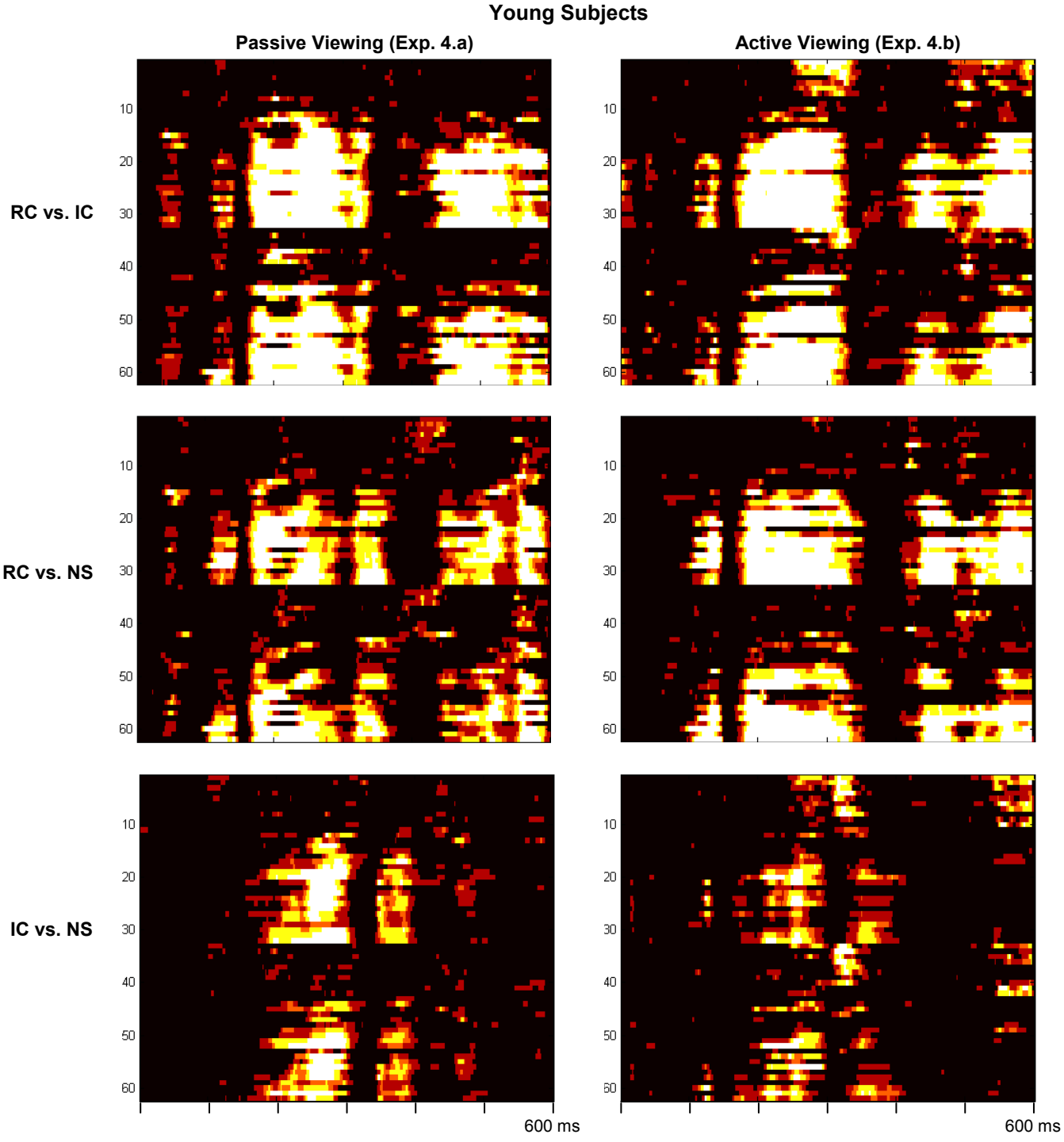

Figure 25: Young participants: results of paired t-tests for differences in VEP amplitude over time for Experiment 4.a) (passive viewing) and Experiment 4.b) (active viewing). y-axis: electrode number (1–62); x-axis: time (0-600 ms post stimulus). Significance level is indicated by increasingly brighter colour: black: not significant; red: $p<0.05$; orange: $p<0.01$; yellow: $p<0.005$; white: $p<0.001$).

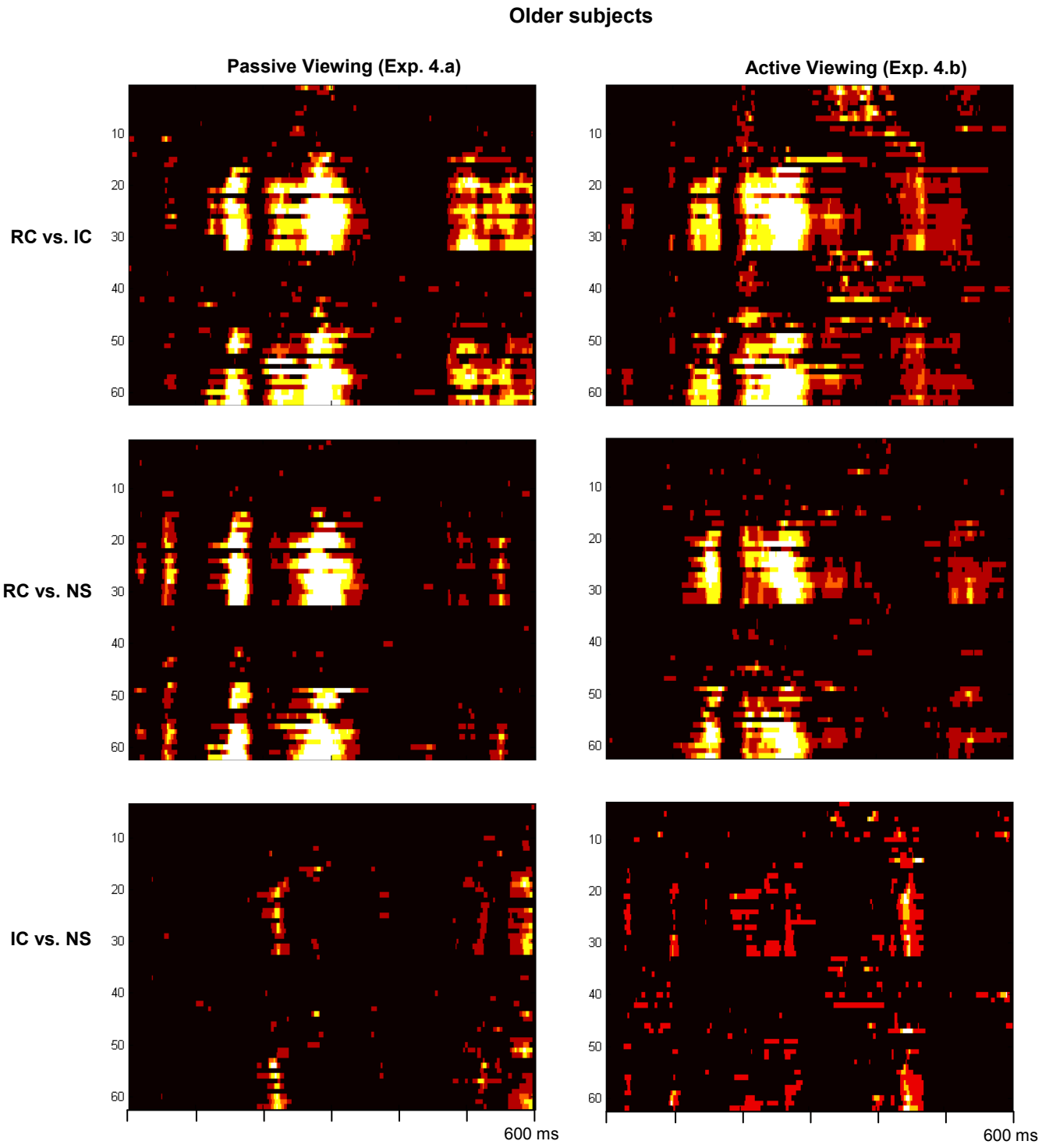

Figure 26: Old participants: results of paired t-tests for differences in VEP amplitude over time for Experiment 4.a) (passive viewing) and Experiment 4.b)(active viewing). y-axis: electrode number (1–62); x-axis: time (0-600 ms post stimulus). Significance level is indicated by increasingly brighter colour: black: not significant; red: $p<0.05$; orange: $p<0.01$; yellow: $p<0.005$; white: $p<0.001$).

Comparing young subjects' results from Experiment 4.a) with those from Experiment 2 (see Figure 12), we observe more or less the same pattern in the comparisons that include RCs: a first cluster of amplitude differences around 90 ms post stimulus, a second around 150 ms post stimulus, and a third between approximately 200 and 400 ms post stimulus. In addition, a period of amplitude differences emerged at around 500 ms post stimulus in Experiment

4.a), which we currently cannot account for. Note that the arrangement of electrodes on the y-axis yields no topographical information, and differs between Experiment 2 and 4.

When it comes to the comparison of ICs with NSs, however, we find a clear differential reaction in the young subjects, one from around 150 ms until 300 ms post stimulus, and another around 400 ms post stimulus. No such differential reaction had been evidenced in Experiment 2 (using larger stimuli), therefore a reduction of stimulus size might indeed facilitate shape identification. It should, however, be kept in mind that no behavioural data or subjective experiences of participants have been surveyed for those two experiments, so it should not be concluded precociously that stimulus sizes below ca. 5° of visual angle were a prerequisite for perceptual binding or that sizes above 5° necessarily impeded it.

Regarding older participants' data, we find a first period of differences around 50 ms post stimulus in the comparisons that include RCs, which most likely reflect physical stimulus properties. A second period of differences occurs around 150 ms post stimulus and a third around 230-350 ms post stimulus in the RC vs. IC/NS comparisons. As in the young participants, another period of differences emerges around 500 ms post stimulus, which we cannot currently account for. In contrast to Experiment 2, we find a relatively distinct period of amplitude differences around 220 ms post stimulus in the IC vs. NS comparison and a late one around 500-600 ms post stimulus. Once again, the fact that we could not evidence statistical differences between IC and NS in Experiment 2 does not imply that ICs were not *perceived*; yet, a reduced stimulus size seems to raise the chances of finding statistically significant differential physiological reactions, for example by reducing the topographical variation of the cortical stimulus representation.

Map series analysis

As a next step, we proceeded to the analysis of microstates (see Experiment 2), to find out whether the differences we observed between stimulus conditions were due to differences in scalp topography of the VEP or rather to differences in the amplitude of the evoked response. Results are displayed in Figure 27 (for young subjects) and Figure 28 (for old subjects).

Passive Viewing (Exp. 4.a)

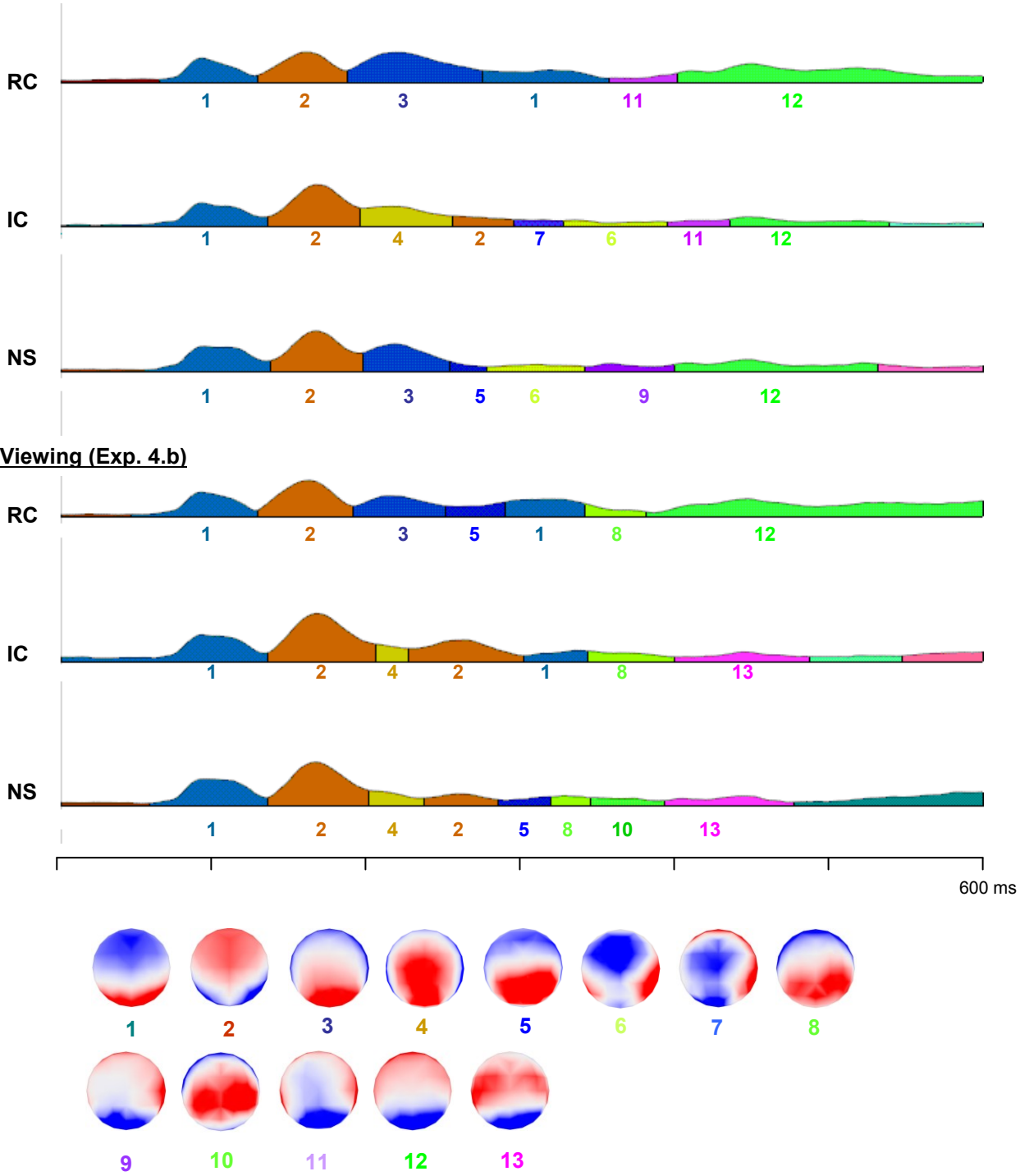

Figure 27: Results of map-series analysis for global field power in young observers for the conditions RC, IC, and NS, viewed passively (top) and actively (middle). The time segments of stable field topography in the six traces are highlighted with different colour fillings under the global field power curve. Corresponding field topographies (for periods of sufficient general GFP-activity) are shown in the bottom part.

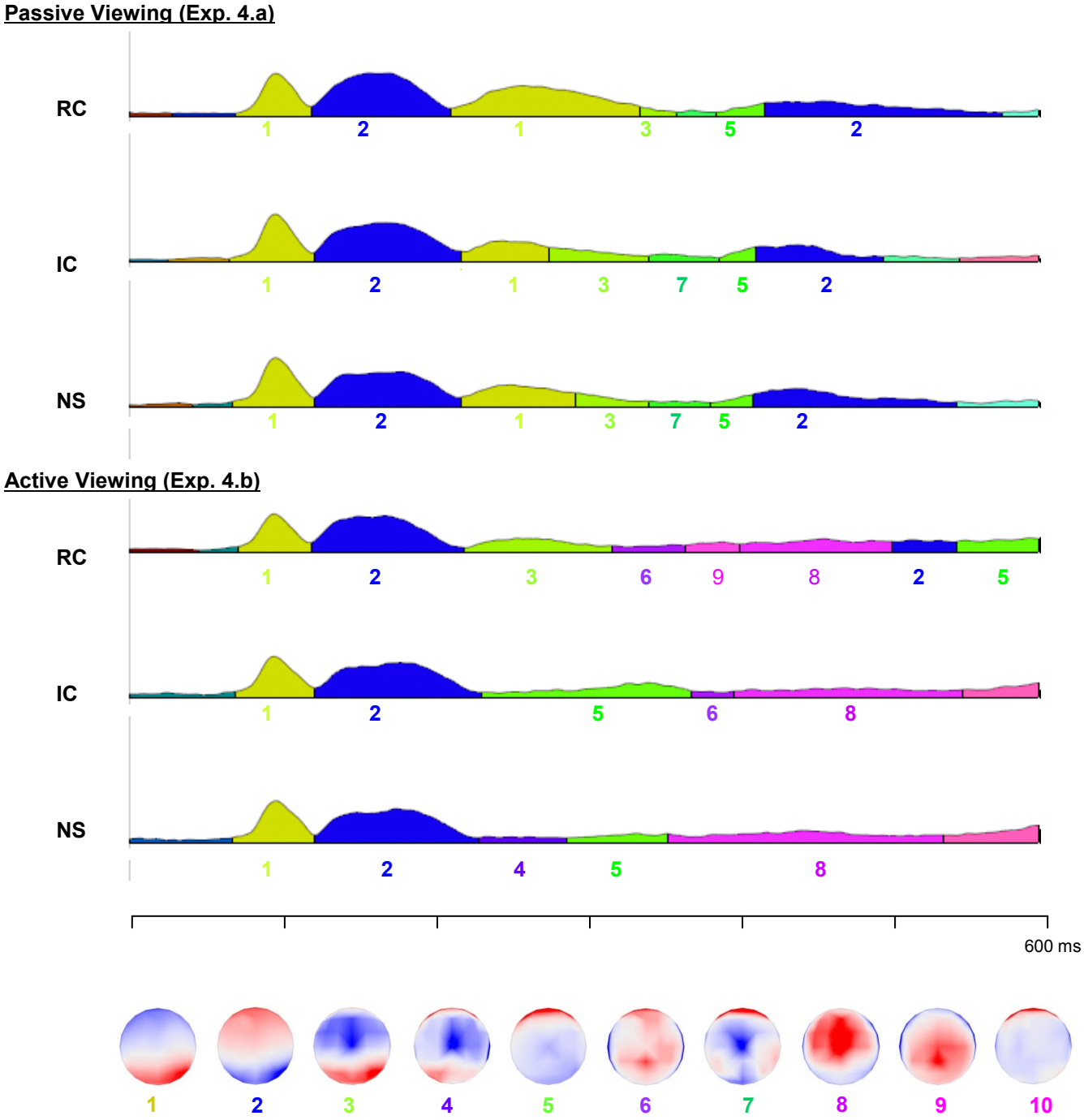

Figure 28: Results of map-series analysis for global field power in older observers for the conditions RC, IC, and NS, viewed passively (top) and actively (middle). The time segments of stable field topography in the six traces are highlighted with different colour fillings under the global field power curve. Corresponding field topographies (for periods of sufficient general GFP-activity) are shown in the bottom part.

As in Experiment 2, we did not find a map that would indicate a specific cortical area being uniquely specialized in IC processing (see also Pegna et al. 2002). Both subject groups show similar patterns of activation independent of stimulus type for the ERP components corresponding to the P100 and N150. Although some diversification appears at later parts of the ERP, no clear picture emerges that would systematically differentiate between

conditions, or between active and passive viewing. In the active paradigm, one might for example have expected some maps with a more frontal focus reflecting the decision process concerned with whether or not the presented stimulus was the target, but our data do not support this.

Slightly fewer different maps of stable activation were identified for old subjects than for the younger ones, which might be the result of the more diffuse patterns of activation in the former. Our observations here would fit well with findings from imaging, suggesting a decrease of functional segregation in brain activity in older people (see for example Grady et al., 1992, 1994).

Analysis of GFP

Since, according to our data, the distinction between shapes was not drawn on the basis of differences in electrical field topography, we proceeded to the analysis of the global field power (GFP) for possible shape discrimination (see Exp. 2 for a description of the procedure). Results are displayed in Figure 29 for young subjects and in Figure 30 for the older participants.

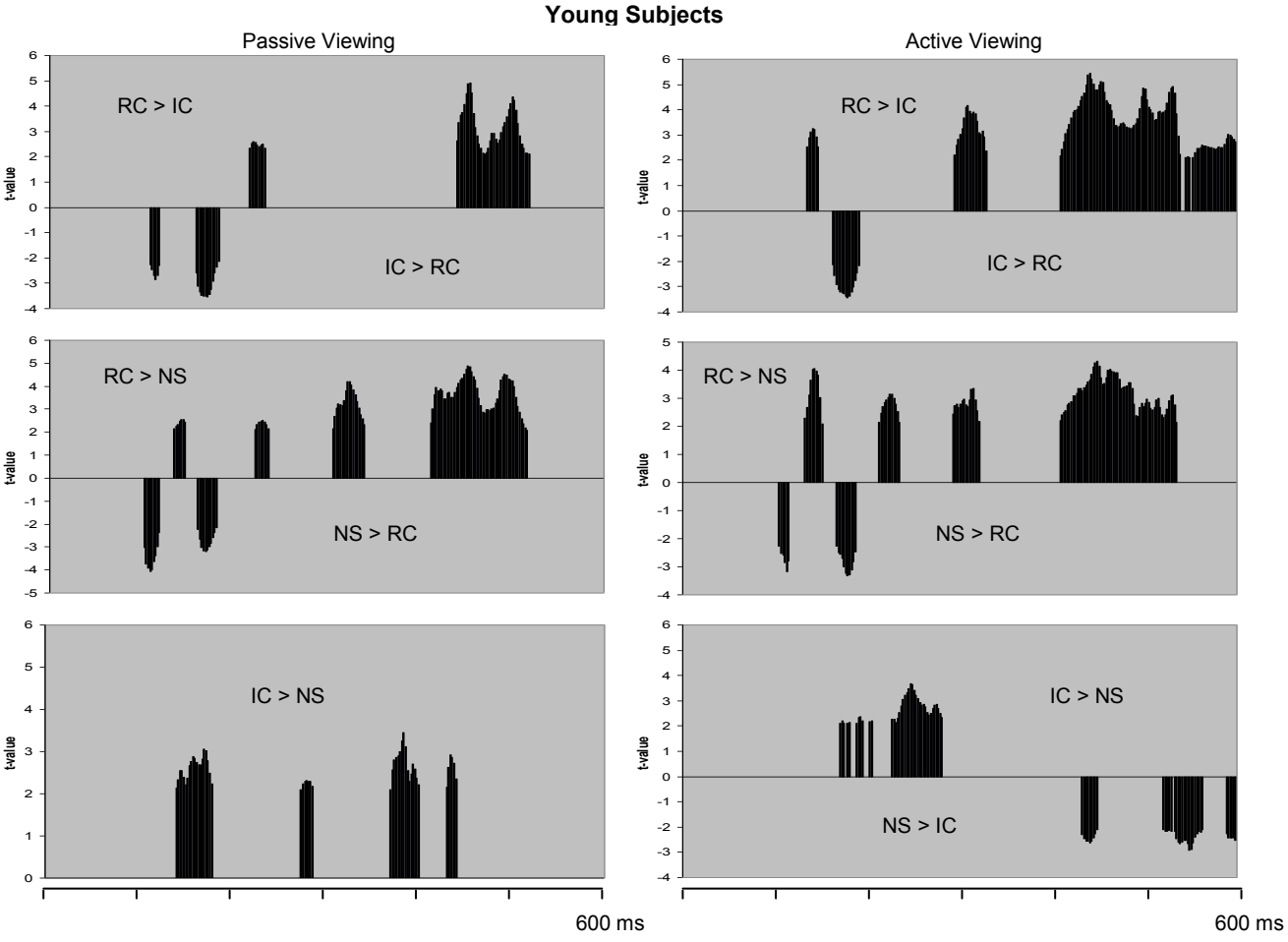

Figure 29: Results of paired t-tests of GFP between conditions for young observers. Only values that are statistically significant ($p<0.05$) over a period of more than 10 ms are shown. Y-axis: t value; X-axis: time post stimulus (ms).

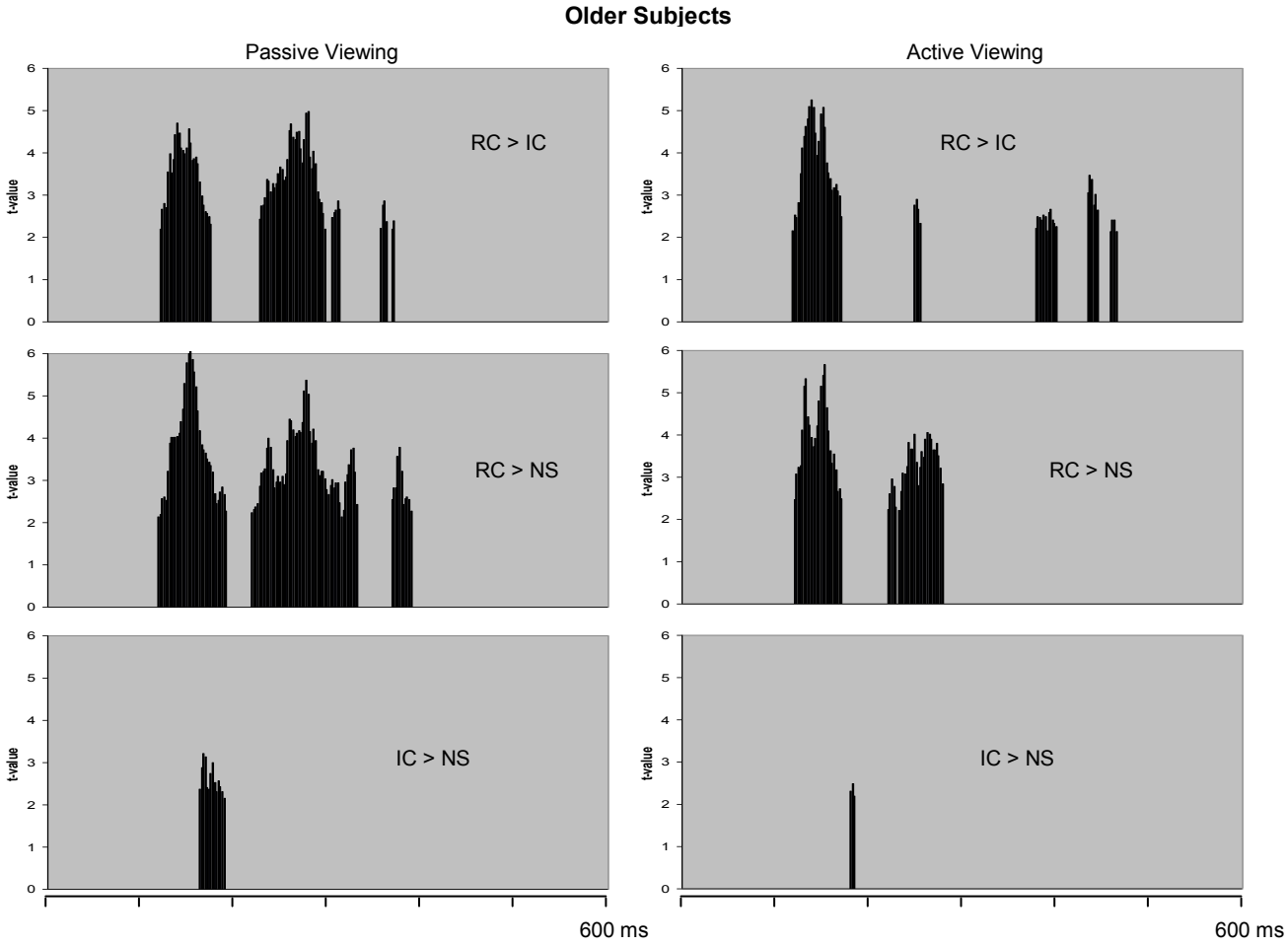

Figure 30: Results of paired t-Tests of GFP between conditions for older observers. Only values that are statistically significant ($p<0.05$) over a period of more than 10 ms are shown. Y-axis: t value; X-axis: time post stimulus (ms).

Here, we replicated our findings from Experiment 2 that young subjects show earlier condition-related differences in GFP than do older observers (around 100 ms post stimulus in young vs. not before 150 ms post stimulus in older subjects). We also replicated that GFP for RCs compared to other conditions would be lower in young, but higher in older observers. In young subjects we find some short periods during which higher GFP for one condition alternates with higher GFP for the contrasting condition, which most likely reflects differences in ERP latency.

Contrasting active and passive viewing, we notice a slight increase in GFP differences, around 400 ms post stimulus. Comparing this with the GFP curves in Fig. 27 and 28, though, it seems that predominantly latency differences account for those late disparities. One may have expected the instruction (to watch out for targets among physically similar stimuli) to increase GFP-differences between conditions, but according to our data this was not the case.

Analysis of peak amplitudes and latencies

As in Experiment 2, we proceeded to an analysis of peak amplitudes and peak latencies, to check whether the condition effects for amplitudes or GFP observed in our t-Tests were the result of actual differences in ERP amplitudes, or were rather the result of condition-related delays of one or more ERP components. As previously, amplitudes and latencies of ERP components P100, N150, and P200 were ascertained for each subject and each condition at six representative electrodes (O1 and O2 for occipital cortex, P3 and P4 for parietal cortex, and PO7 and PO8 for parieto-occipital cortex).

Peak Amplitudes

P100 Amplitude

Subjects' P100 amplitude values were submitted to a four-way 2×3×3×2 repeated-measures ANOVA with the factors *group* (young / old), *condition* (RC / IC / NS), *electrode position* (occipital / parietal / parieto-occipital), and electrode *side* (left / right). Subsequently, post-hoc paired t-Tests were performed to gain insight on the nature of possible condition effects. The same statistical procedure was applied for the subsequent analyses. For the sake of clarity, data of the passive (Exp. 4.a) and active (Exp. 4.b) viewing paradigm were analyzed separately.

a) Passive Viewing

Our results yielded a significant main effect for *position* (F=20.527; p=0.000), with highest amplitudes at parieto-occipital sites, followed by occipital electrodes, and comparably low amplitudes at parietal electrodes. We also found a *condition*×*position* (F=5.541; p=0.002) interaction, showing that condition differences occurred predominantly at occipital and parieto-occipital electrodes. However, a further interaction *condition* × *position* × *group* (F=4.723; p=0.004) indicated that mostly the young subjects contributed to the *condition* × *position* interaction mentioned above, while older subjects hardly showed condition differences at the P100. Finally, we found a *position* × *side* interaction (F=14.438; p=0.000) with higher right-sided amplitudes at parietal and parieto-occipital electrodes, while amplitudes at occipital electrodes were slightly higher at the left side.

Our post-hoc tests revealed that only the occipital electrodes in young subjects responded differentially and only when RCs were implied. This probably reflects differences in physical stimulus properties.

	Passive Viewing: P100 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.046* IC>RC	p=0.017* NS>RC	p=0.766	O2	p=0.002* IC>RC	p=0.000*** NS>RC	p=0.809
	P3	p=0.822	p=0.487	p=0.271	P4	p=0.114	p=0.169	p=0.928
	PO7	p=0.156	p=0.091	p=0.813	PO8	p=0.282	p=0.460	p=0.782
Old	O1	p=0.914	p=0.840	p=0.900	O2	p=0.381	p=0.941	p=0.322
	P3	p=0.555	p=0.798	p=0.756	P4	p=0.752	p=0.778	p=0.571
	PO7	p=0.960	p=0.792	p=0.700	PO8	p=0.446	p=0.683	p=0.280

Table 13: Post-hoc paired t-Tests for P100 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown.

b) Active Viewing

In the active-viewing paradigm, we found the same significant main effect for *position* (F=17.939; p=0.000; parieto-occipital > occipital >> parietal; see above) as in the passive paradigm, as well as a *position* x *side* interaction (F=12.461; p=0.000) of the same kind as in the passive paradigm (higher amplitudes at right-sided parietal and parieto-occipital electrodes, higher left-sided amplitudes at occipital electrodes).

A significant main effect for condition (F=4.921; p=0.013) indicated highest peak amplitudes for NSs, followed by RCs, and ICs. Condition effects were more distinct at parieto-occipital and parietal sites, as was indicated by a *condition* x *position* interaction (F=5.428; p=0.002). We found that young subjects had higher amplitudes for IC and NS than older observers, while amplitudes for RC were relatively similar in both groups (*condition* x *group* interaction; F=6.513; p=0.004). Another interaction condition x position x group (F=9.676: p=0.000) revealed that amplitude relations between conditions were not the same in the two subject groups: while in older subjects amplitudes for RCs were higher than for NSs and ICs at all electrode positions, younger subjects' amplitudes for RCs were lower than for other conditions, this effect being strongest at occipital electrodes.

In our post-hoc comparisons, we found considerably more significant differential effects as in the passive viewing paradigm. Especially the older participants reacted with amplitude differences between conditions when ICs were implied.

	Active Viewing: P100 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.169	p=0.014* NS>RC	p=0.063	O2	p=0.003*** IC>RC	p=0.000** NS>RC	p=0.063
	P3	p=0.669	p=0.447	p=0.627	P4	p=0.650	p=0.008** NS>RC	p=0.035* NS>IC
	PO7	p=0.368	p=0.111	p=0.282	PO8	p=0.135	p=0.001*** NS>RC	p=0.310
Old	O1	p=0.006*** RC>IC	p=0.442	p=0.003*** NS>IC	O2	p=0.045*** RC>IC	p=0.447	p=0.060
	P3	p=0.015* RC>IC	p=0.612	p=0.007** NS>IC	P4	p=0.070	p=0.666	p=0.114
	PO7	p=0.002*** RC>IC	p=0.332	p=0.003*** NS>IC	PO8	p=0.046* RC>IC	p=0.360	p=0.071

Table 14: Post-hoc paired t-Tests for P100 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown.

N150 Amplitude

a) Passive Viewing

For the amplitude of the N150 we found a significant main effect for *electrode position* (F=13.776; p=0.000) with highest (negative) amplitudes at parieto-occipital sites, followed by occipital, and lowest at parietal sites. A pronounced *position* x *side* interaction (F=14.490; p=0.000) indicated that amplitudes were higher in the right hemisphere at parietal and parieto-occipital electrodes, whereas little side differences were seen at occipital electrodes. In both groups, highest amplitudes were at parieto-occipital, and lowest at parietal electrodes, the position differences being, however, more pronounced in young subjects (*group* x *position* interaction; F=4.652; p=0.016). While young subjects' amplitudes for RCs were relatively lower than for other conditions, the opposite was the case in the older group (*condition* x *group* interaction; F=13.440; p=0.000), see also Table 15.

	Passive Viewing: N150 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.008** IC>RC	p=0.011* NS>RC	p=0.096	O2	p=0.004* IC>RC	p=0.010* NS>RC	p=0.020* IC>NS
	P3	p=0.003*** IC>RC	p=0.005** NS>RC	p=0.167	P4	p=0.001*** IC>RC	p=0.003*** NS>RC	p=0.068
	PO7	p=0.007** IC>RC	p=0.018* NS>RC	p=0.094	PO8	p=0.003*** IC>RC	p=0.041* NS>RC	p=0.060
Old	O1	p=0.017* RC>IC	p=0.003*** RC>NS	p=0.340	O2	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.272
	P3	p=0.529	p=0.479	p=0.848	P4	p=0.003*** RC>IC	p=0.000*** RC>NS	p=0.142
	PO7	p=0.003*** RC>IC	p=0.002*** RC>NS	p=0.697	PO8	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.286

Table 15: Post-hoc paired t-Tests for N150 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown. Note that the negative polarity of this ERP component has been taken into account (NS > RC would for example mean that NS had a higher negative amplitude than RC).

b) Active Viewing

In the active paradigm, the amplitude differences between young and old subjects reached significance level (main effect for *group*; F=4.885; p=0.034; higher amplitudes in the young group). As in the passive paradigm, we found a significant main effect for *position* (F=10.854; p=0.000; highest amplitudes at parieto-occipital electrodes, lowest at parietal electrodes). A significant main effect for *condition* (F=7.764; p=0.002) indicated highest amplitudes for ICs and only small differences between RCs and NSs. A *group* x *condition* interaction (F=6.363; p=0.004) revealed that differences in amplitude between conditions were larger in the younger group. Finally, as in the passive paradigm, interhemispheric differences were much stronger at parietal and parieto-occipital electrodes than at occipital ones (*position* x *side* interaction; F=9.971; p=0.000).

In our post-hoc comparisons (see Table 16) we almost consistently saw significant differences between ICs and NSs, which was not the case in the passive paradigm. Since the difference between RCs and NSs does not increase to the same degree, this most likely represents more than a simple target effect.

	Active Viewing: N150 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.004** IC>RC	p=0.145	p=0.010* IC>NS	O2	p=0.001** IC>RC	p=0.126	p=0.002*** IC>NS
	P3	p=0.006** IC>RC	p=0.184	p=0.076	P4	p=0.001*** IC>RC	p=0.034* NS>RC	p=0.020* IC>NS
	PO7	p=0.004*** IC>RC	p=0.163	p=0.020* IC>NS	PO8	p=0.006** IC>RC	p=0.102	p=0.039* IC>NS
Old	O1	p=0.056	p=0.006** RC>NS	p=0.019* IC>NS	O2	p=0.808	p=0.054	p=0.005 IC>NS
	P3	p=0.118	p=0.023* RC>NS	p=0.040* IC>NS	P4	p=0.477	p=0.029* RC>NS	p=0.008** IC>NS
	PO7	p=0.087	p=0.024* RC>NS	p=0.065	PO8	p=0.752	p=0.079	p=0.002*** IC>NS

Table 16: Post-hoc paired t-Tests for N150 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown. Note that the negative polarity of this ERP component has been taken into account (NS > RC would for example mean that NS had a higher negative amplitude than RC).

P200 Amplitude

a) Passive Viewing

For the P200 amplitude we found a significant main effect for *condition* (F=51.450; p=0.000); amplitudes for RCs were considerably higher than for NSs, and lowest for ICs. Furthermore, a *condition* x *position* interaction (F=6.153; p=0.001) indicated that condition differences were stronger at occipital and parieto-occipital than at parietal electrodes. Differences between RCs and ICs were stronger in young subjects at occipital and parieto-occipital electrodes, the difference between RCs and NSs, however, was more pronounced in the older participants

(*condition* x *position* x side *interaction*; F=3.065; p=0.030). At parietal electrodes, amplitudes were higher in the right hemisphere, while no side differences occurred at parietal or parieto-occipital electrodes (*position* x *side* interaction; F=7.050; p=0.003).

Although we did not find a significant *condition* x *group* interaction for the P200 amplitude in passive viewing, our post-hoc comparisons reveal that young subjects show an IC-effect (significant difference between ICs and NSs) at this ERP component, while older subjects do not.

	Passive Viewing: P200 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.011* NS>IC	O2	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.121
	P3	p=0.000*** RC>IC	p=0.001*** RC>NS	p=0.004*** NS>IC	P4	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.039* NS>IC
	PO7	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.002*** NS>IC	PO8	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.001*** NS>IC
Old	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.122	O2	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.368
	P3	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.161	P4	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.416
	PO7	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.182	PO8	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.675

Table 17: Post-hoc paired t-Tests for P200 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown.

b) Active Viewing

As in the passive paradigm, amplitudes for RCs were higher than for NSs, followed by ICs (significant main effect for *condition*; F=72.679; p=0.000). Condition effects were more pronounced in the young subjects, as indicated by a *condition* x *group* interaction (F=3.915; p=0.030). Young subjects had higher ERP amplitudes than old subjects at parietal and occipital electrodes (*position* x *group* interaction; F=3.471; p=0.042). As in the active paradigm, a *condition* x *position* interaction (F=3.703; p=0.014) indicated that condition effects were stronger at occipital and parieto-occipital electrodes, especially in the left hemisphere (*condition* x *position* x *side* interaction; F=4.726; p=0.004).

Our post-hoc tests show a similar pattern as in the passive paradigm: pronounced differences between RCs and other conditions, and a comparably weaker IC effect, especially in older subjects, where no IC effect can be evidenced.

	Active Viewing: P200 peak amplitude – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.190	O2	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.190
	P3	p=0.000*** RC>IC	p=0.001*** RC>NS	p=0.092	P4	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.044* NS>IC
	PO7	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.014* NS>IC	PO8	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.030* NS>IC
Old	O1	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.236	O2	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.117
	P3	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.207	P4	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.337
	PO7	p=0.001*** RC>IC	p=0.000*** RC>NS	p=0.401	PO8	p=0.000*** RC>IC	p=0.000*** RC>NS	p=0.579

Table 18: Post-hoc paired t-Tests for P200 peak amplitude between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown.

Peak Latencies

P100 Latency

a) Passive Viewing

For the latency of the P100 component we found a main effect for *condition* (F=4.627; p=0.017), with shortest latencies for RCs and comparable latencies for ICs and NSs. A *condition* x *group* interaction (F=4.506; p=0.018) put, however, forward that this effect only occurred in the group of young observers (see also Table 19). The latency difference between young and old subjects (earlier peaks in older subjects) that we had already observed as a tendency in Experiment 2, reached significance level here (significant main effect for *group*; F=7.278; p=0.011).

	Passive Viewing: P100 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.070	p=0.352	p=0.166	O2	p=0.713	p=0.041* RC→NS	p=0.070
	P3	p=0.339	p=0.737	p=0.602	P4	p=0.016* RC→IC	p=0.003*** RC→IC	p=0.417
	PO7	p=0.008** RC→IC	p=0.107	p=0.286	PO8	p=0.013* RC→IC	p=0.009** RC→NS	p=0.770
Old	O1	p=0.332	p=0.835	p=0.382	O2	p=0.668	p=0.718	p=1.000
	P3	p=0.636	p=0.280	p=0.385	P4	p=0.817	p=0.508	p=0.332
	PO7	p=0.805	p=0.508	p=0.260	PO8	p=0.735	p=1.000	p=0.668

Table 19: Post-hoc paired t-Tests for P100 peak latency between stimulus conditions. Significance level (p-value; * p<0.05; ** p<0.01; *** p<0.005) and quality of difference are shown (RC→IC for example means that for RC the peak occurs earlier than for IC).

b) Active Viewing

As in the passive paradigm, the P100 peaked earlier in old subjects (significant main effect for *group*; F=7.656; p=0.009). At parietal and parieto-occipital electrodes, the peaks occurred earlier in the right hemisphere (*position* x *side* interaction; F=3.319; p=0.048), with exception of occipital electrodes in young subjects, where the left side peaked about 2 ms before the right side (*position* x *side* x *group* interaction; F=4.973; p=0.013).

Our post-hoc tests confirm that the P100 from RCs occurs earliest among the three stimulus conditions, this effect occurring predominantly in the right hemisphere of the young subjects.

	Active Viewing: P100 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.789	p=0.789	p=0.963	O2	p=0.058	p=0.059	p=0.574
	P3	p=0.552	p=0.484	p=0.752	P4	p=0.048* RC→IC	p=0.059	p=0.603
	PO7	p=0.853	p=0.441	p=0.256	PO8	p=0.015* RC→IC	p=0.027* RC→NS	p=0.807
Old	O1	p=0.197	p=0.287	p=0.397	O2	p=0.223	p=0.410	p=0.285
	P3	p=0.064	p=0.007** RC→NS	p=0.837	P4	p=0.166	p=0.466	p=0.314
	PO7	p=0.373	p=0.351	p=0.655	PO8	p=0.128	p=0.086	p=0.359

Table 20: Post-hoc paired t-Tests for P100 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

N150 Latency

a) Passive Viewing

In the passive paradigm, shortest latencies were found for RCs, followed by NSs, and longest latencies for ICs (main effect for *condition*; F=15.047; p=0.000). A *position* x *side* interaction (F=3.381; p=0.030) indicated that peaks occurred earlier in the right hemisphere at parietal electrodes, but that the left side peaked earlier at occipital and parieto-occipital electrodes.

Our post-hoc comparisons indicated that the above-mentioned condition effect stemmed mostly from the early peaking of RCs.

	Passive Viewing: N150 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.000*** RC→IC	p=0.001*** RC→NS	p=0.880	O2	p=0.000*** RC→IC	p=0.001 RC→NS	p=0.693
	P3	p=0.009** RC→IC	p=0.010* RC→NS	p=0.621	P4	p=0.000*** RC→IC	p=0.001*** RC→NS	p=0.297
	PO7	p=0.000*** RC→IC	p=0.003*** RC→NS	p=0.629	PO8	p=0.001*** RC→IC	p=0.002*** RC→NS	p=0.676
Old	O1	p=0.037* RC→IC	p=0.265	p=0.135	O2	p=0.003*** RC→IC	p=0.156	p=0.098
	P3	p=0.592	p=0.490	p=0.184	P4	p=0.029* RC→IC	p=0.174	p=0.384
	PO7	p=0.133	p=0.283	p=0.651	PO8	p=0.004*** RC→IC	p=0.245	p=0.089

Table 21: Post-hoc paired t-Tests for P100 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

b) Active Viewing

In the active viewing paradigm, we found the same *condition* main effect (F=15.047; p=0.000) as in the passive paradigm; peaks of RCs preceded the other conditions by almost 8 ms, while little differences appeared between ICs and NSs (see also post-hoc tests in Table 22). We furthermore found a *position x side* interaction (F=6.101; p=0.005) that indicated that the right hemisphere peaked earlier at parietal electrodes, the left hemisphere at occipital electrodes, and at about the same time at parieto-occipital electrodes.

In our post-hoc tests we can see that the difference between RCs and NSs increases in older subjects as compared to the passive paradigm, which might reflect a target effect; on the other hand, this is not the case for the difference between ICs and NSs, so another interpretation of these findings might be required.

	Active Viewing: N150 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.006** RC→IC	p=0.003*** RC→NS	p=0.599	O2	p=0.031* RC→IC	p=0.000 RC→NS	p=0.686
	P3	p=0.058	p=0.015* RC→NS	p=0.642	P4	p=0.000*** RC→IC	p=0.000*** RC→NS	p=0.679
	PO7	p=0.031* RC→IC	p=0.006** RC→NS	p=0.276	PO8	p=0.001*** RC→IC	p=0.000*** RC→NS	p=0.348
Old	O1	p=0.053	p=0.037* RC→NS	p=1.000	O2	p=0.040* RC→IC	p=0.026* RC→NS	p=0.258
	P3	p=0.073	p=0.333	p=0.559	P4	p=0.020* RC→IC	p=0.053	p=0.703
	PO7	p=0.042* RC→IC	p=0.013* RC→NS	p=0.886	PO8	p=0.052	p=0.040* RC→NS	p=0.409

Table 22: Post-hoc paired t-Tests for N150 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

P200 Latency

a) Passive Viewing

The earliest peaks for the P200 in passive viewing occurred at occipital electrodes, then at parieto-occipital electrodes, and finally at parietal electrodes (significant main effect for *condition*; F=4.761; p=0.015). A *position* x *group* interaction (F=3.847; p=0.031) revealed, however, that only the young subjects' latencies varied noteworthy between electrode positions. Finally, a *condition* x *position* interaction (F=3.194; p=0.026) indicated that differences in latency between conditions varied between electrodes: at occipital electrodes, RCs peaked earlier than NSs, and considerably earlier than ICs. At parieto-occipital electrodes, the difference between RCs and the other conditions was larger than at the occipital electrodes, while the difference between ICs and NSs was comparably smaller. At parietal electrodes, finally, latency differences were negligible.

	Passive Viewing: P200 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.062	p=0.030* RC→NS	p=0.636	O2	p=0.161	p=1.000	p=0.435
	P3	p=0.851	p=0.146	p=0.563	P4	p=0.389	p=0.680	p=0.295
	PO7	p=0.007** RC→IC	p=0.003*** RC→NS	p=0.698	PO8	p=0.768	p=0.433	p=0.668
Old	O1	p=0.737	p=0.642	p=1.000	O2	p=0.084	p=0.561	p=0.036* NS→IC
	P3	p=0.806	p=0.314	p=0.578	P4	p=0.181	p=0.863	p=0.183
	PO7	p=0.983	p=0.886	p=0.920	PO8	p=0.053	p=0.576	p=0.180

Table 23: Post-hoc paired t-Tests for P200 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

b) Active Viewing

In the active viewing paradigm, we did not find any significant main effects or interactions.

	Active Viewing: P200 peak latency – post-hoc comparisons							
	Left hemisphere				Right hemisphere			
	Electrode	RC vs. IC	RC vs. NS	IC vs. NS	Electrode	RC vs. IC	RC vs. NS	IC vs. NS
Young	O1	p=0.525	p=0.971	p=0.496	O2	p=0.972	p=0.909	p=0.882
	P3	p=0.370	p=0.733	p=0.594	P4	p=0.613	p=0.922	p=0.513
	PO7	p=0.866	p=0.961	p=0.861	PO8	p=0.897	p=0.247	p=0.277
Old	O1	p=0.366	p=0.821	p=0.546	O2	p=0.612	p=0.100	p=0.060
	P3	p=0.619	p=0.135	p=0.151	P4	p=0.227	p=0.491	p=0.410
	PO7	p=0.386	p=0.942	p=0.496	PO8	p=0.227	p=0.238	p=0.843

Table 24: Post-hoc paired t-Tests for P200 peak latencies between stimulus conditions (* p<0.05; ** p<0.01; *** p<0.005).

3.4.4. Discussion

In Experiment 4.a) we tested whether reducing the eccentricity of the stimulus components would facilitate visual binding, or, in other words, whether stimulus size had been the central factor for not finding a noteworthy IC effect in Experiment 2. As mentioned before, due to differences in the overall luminance, we will not explicitly discuss comparisons that include the RC condition.

When we compare the t-tests on VEP amplitude over time (Figure 12 for Exp. 2 and Figure 25 and 26 for Exp. 4), we find a noteworthy increase of time periods showing significant amplitude differences between the conditions, especially in the young observers. Both subject groups display amplitude differences between ICs and NSs around 200 ms post stimulus; these differences are more pronounced in the younger subjects and last over a longer period. In our analysis of VEP peaks we find significant differences at the N150 at electrode O2 in the young observers, and other right-sided electrodes approach significance level (see Table 15). The p-values for the left-sided electrodes (see Table 15) suggest that in a larger sample the amplitude differences might have reached significance. In the older observers, however, it does not seem that a reduced stimulus size would increase amplitude differences between ICs and NSs. For the P200 peak, we find an IC effect at most of the tested electrodes in the young observers (see Table 17), but no such effect in the older participants.

As for the analysis of the global field power (see Figure 14, 29, and 30), it does not appear that reducing the stimulus size would have a considerable effect. In young subjects we observe some more periods with significant GFP differences in Experiment 4.a) as compared to Experiment 2 and in the older subjects less in Experiment 4.a) than in Experiment 2. It should, however, be kept in mind that this way of displaying results depends largely on the applied criteria (for example the number of consecutive time frames containing significant GFP differences), and we currently do not have the impression of seeing an important effect here.

In Experiment 2, the results of our map series analysis (see Figure 13) did not hint that specific cortical areas would be responsible for the processing of certain stimulus types, which is in accordance with previous findings (see the Discussion for Experiment 2). As can be seen in the map-series analyses in Figure 27 and 28, a reduction of the eccentricity of the stimulus components does not change anything with respect to the stimulus-related topography of the electrophysiological signal.

Taken together, our insults indicate that IC perception is facilitated when the stimulus is presented in the foveal area. Particularly in young subjects, we found a noteworthy increase

in differential electrophysiological reactions between ICs and NSs in Experiment 4.a) as compared to Experiment 2. For the older observers, however, we could not confirm this increase in stimulus-related differential activity. As mentioned in the discussion of Experiment 2, the lack of a differential reaction does not forcibly mean that ICs were not perceived, and, conversely, the fact that we did find a differential reaction in Experiment 4.a) does not forcibly mean that ICs were perceived here. To answer this, it would require an experimental setup that directly assesses the electrophysiological correlate of the subjective qualities of ICs (such as subjective brightness or stratification as compared to control stimuli), which we had not tried. Still, according to our EEG data, it seems more likely that our young subjects perceived ICs in Experiment 4.a) than that they did in Experiment 2.

As for our older observers, our results in Experiment 4.a) could either signify that a reduction of stimulus size to foveal vision is still not sufficient to evoke the perception of ICs. On the other hand, we can not rule out the possibility that the perception of IC was intact in our older observers, but that a statistically significant IC effect could not be achieved due to inter-individual differences (i.e., a decrease of functional segregation) in the cortical activation pattern. Yet, our observations in Experiment 1 suggest that the perception of ICs is indeed affected by the ageing process; the prolonged response times could reflect a delay of the processes implied in IC perception or a qualitative decomposition of the subjective percept, which would be compensated for by cognitive strategies (as indicated by prolonged response times in the absence of increased error rates). Our EEG data in Experiment 2 and 4.a) would fit with this idea.

4. General discussion

In this dissertation a series of experiments were presented, in which we tried to asses the effects of age, attention, and stimulus size on the perception of illusory contours (ICs). The first two experiments were explorative in nature, and the subsequent ones were based on the findings we observed there.

Our first experiment was psychophysical in nature; it aimed at exploring whether the perception of illusory contours was affected by normal brain aging. We found that the reaction time required for the discrimination of ICs – in contrast to real contour stimuli – significantly increased with advancing age. Only the youngest subject group responded with the same rapidity to ICs and RCs alike, as should be expected if ICs are processed pre-attentively, as postulated by several authors (e.g. Senkowski et al. 2005, Vuilleumier & Landis 1998, Davis & Driver 1994). A general age-related slowing could not account for this finding, since some of our oldest participants (71-90 years) partially reached better response times for the control conditions than some of the younger subject groups. Although little is known about IC perception in older participants, certain deficits were to be expected, since many visual functions are known to be altered by normal aging (see for example McKendrick et al. 2010, Del Viva & Agostini, 2007, Li & Lindenberger 2002; Sekuler & Sekuler 2000, Anderson et al. 2000, Baltes & Lindenberger 1997; Cabeza et al. 1997, Madden et al. 1996, Madden & Allen 1991; Weale 1963). The decline in visual binding which we observed here, seems to start relatively early in life, since already from the age of 30 years on, participants needed considerably more time in the IC condition.

In our second experiment, we searched for an electrophysiological correlate that might account for our observations in the psychophysical experiment. In our non-response EEG paradigm we could not, however, replicate previous results concerning the so-called IC-effect, i.e. a differential reaction between IC- and NS-stimuli, occurring around the N150, that is thought to reflect the perception of the « Gestalt » (Murray et al. 2004, 2002; Kruggel et al, 2001; Herrmann & Bosch 2001; Murray et al. 2002; Halgren et al. 2003; Korshunova et al. 1999). While both young and older viewers' VEPs clearly differed between RC stimuli and the other two conditions, we found no differential VEP reaction between IC and NS stimuli that would have corresponded to the viewers perceiving the Kanizsa triangle in this task. Although previous psychophysical research had shown that visual binding (as required in IC perception) can be achieved up to distances of 13 deg of visual angle between inducers (Ringach & Shapley, 1996), we surmised that under the instruction of fixating the central cross, the inducing elements might have been placed too eccentrically to support a figural

binding. Some studies on the local / global processing of stimulus features (typically investigated with so-called Navon letters; Navon, 1977) have reported a local precedence effect when global stimuli were larger than 6 deg of visual angle in young (Kinchla & Wolfe, 1979), as well as in older subjects (Slavin et al., 2002; Massman et al. 1993). In our case this would mean that subjects might have focussed the local element (the fixation cross) while more or less ignoring the global shape.

In our second EEG experiment (Experiment 4.a) we therefore decreased stimulus size to 4 deg of visual angle while keeping all other parameters constant. Although stimulus size was now in the same range as in most other published EEG studies on Kanizsa type ICs, we still found only a rather feeble IC effect in young subjects (where, except for one electrode, the difference between ICs and NSs failed to reach significance), and no differential reaction in the older observers. Only when we modified the instruction in Experiment 4.b), forcing subjects to process the stimuli on a global level, did we find a distinct IC effect in both the young and the older observers.

This study has been the first to directly contrast an active and a passive viewing paradigm with Kanizsa-type stimuli in a within-subject design. In the active viewing paradigm we found enlarged ERP components in all conditions, which goes in line with previous EEG findings in the context of spatial attention (see for example Hopfinger et al. 2004; Di Russo et al. 2003), yet the increase of differential stimulus-related activity was striking. Both young and older subjects now showed the differential reaction between IC and NS stimuli, which has been associated with the perception of the “Gestalt” (Kruggel et al, 2001; Herrmann & Bosch 2001; Murray et al. 2004, 2002; Halgren et al. 2003). Together with the fact that both young and older observers correctly reported the number of the deviant target stimuli, we suppose that the illusory forms were really perceived in this experiment.

So, is attention now an indispensable factor in the perception of ICs? In our last EEG experiment *attention* was clearly the factor that made the difference. Yet, certain issues should be discussed before generalizing this finding. All previous EEG studies on ICs, except for the one of Korshunova (1999), had been based on active viewing paradigms, i.e., subjects had to respond to the presented stimuli, for example by pressing corresponding buttons. Only in the study of Korshunova (1999), subjects were simply instructed to gaze at a fixation point in the centre of the illusory figure (or non-shape), just as in our passive viewing experiments. In contrast to the study of Korshunova (1999), however, the stimulus material we had used was more complex. We had introduced additional circular elements in order not to precociously induce a triangular form. This might have proven as a special handicap for the older observers who often show a diminished capacity to ignore non-pertinent information

(for example Scialfa et al. 1998; Scialfa et al. 1994; Gilmore et al. 1985). Furthermore, the support ratio of our illusory shape was smaller than that in the Korshunova study, which might have impeded the IC perception (see for example Liinasuo et al. 1997; Kojo et al. 1993). It is therefore possible that we might have found stronger effects – even in a passive viewing paradigm – if we had made our IC stimulus material more salient, for example by enlarging the support ratio or removing the additional circular elements that were not part of the illusory or real form, respectively non-shape. The enormous increase of differential electrophysiological activity that we observed in our active viewing paradigm, does, however, speak in favour of an important impact of top-down influences in visual perception.

The central question of this study had been whether the perception of ICs was altered in the course of normal brain aging. Our data from the psychophysical experiments showed a deterioration of response times in the IC condition that proportionally increased with advancing age. It is unlikely that this resulted from a complete failure to perceive the illusory form, since error rates were slightly elevated in the oldest group, but not to a degree that would suggest that the IC stimuli were not perceived at all. When we gave the instructions for the psychophysical experiments to our older subjects, it happened on several occasions that they did not perceive the Kanizsa triangle instantly. They did so, however, when the illusory shape was pointed out ("oh – now I see it – it's brighter than the background"). The subjective nature of the deficits in IC processing which we found in our older subjects remains unclear. Do the illusory shapes have the same subjective quality (for example enhanced brightness and stratification) as in the younger observers, but their processing is simply delayed? Or are there qualitative differences, i.e., the subjective percept is weaker than in younger observers? Or are the illusory shapes not perceived by a bottom-up process, but their presence is inferred by top-down mechanisms?

Our EEG data in the active viewing paradigm speak against a total failure of IC perception in older observers, since the IC effect occurred during early components of the VEP (equal to the young subjects), which are associated with early steps of visual cortical processing. So why did they not show an IC effect in the passive viewing paradigm, although the stimulus material was identical to that in the active paradigm? One possible explanation could lie in the reduction of the useful field of view that has been observed in older people (Ball et al. 2002; Kosslyn et al. 1999; Sekuler et al. 2000; Scialfa et al. 1987), which might have caused them to process the local element (the fixation cross) instead of the global element (the illusory shape) (see Slavin et al., 2002; Massman et al. 1993). Furthermore, it was reported that older observers were not able to perform linkages between unconnected elements over the same distances as young people in contour integration tasks (McKendrick et al. 2010).

This could explain why we found an (although not very pronounced) IC effect in the young, but not the older observers in the passive viewing paradigm.

The age-related deficits in closed contour formation have been associated with alterations of the anatomical or functional connectivity of long-range connections in the striate cortex (study on rhesus monkeys by Peters et al. 2001; cited by McKendrick et al. 2010), as well as delays of signal timing, or aberrant spontaneous neural firing in V1 and V2 (corresponding to humans' striate and prestriate cortex) (primate studies; Whang et al. 2005; Leventhal et al. 2003; cited by McKendrick et al. 2010). McKendrick and collaborators suggested that "aberrant neural firing and timing delays in the aged brain might result in a decrease in neural synchronization that influences performance on tasks that require the grouping of perceptual information across space" (McKendrick et al. 2010, p.7). We assume that such a process could also account for the deficits we observed for the perception of ICs in our older participants.

In general, our EEG data agree with findings from functional imaging, which suggest a reorganization of the cortical functional circuitry in the course of the aging process; several studies provided evidence for a less efficient use of occipital (prestriate) areas during visual tasks in elderly subjects (Grady et al. 1994; Cabeza et al. 2004). In addition, elderly subjects were reported to recruit areas which were not (or less) activated by young subjects in these tasks, such as the frontal cortex (see also Esposito et al. 1999 for visuo-cognitive tasks). Our results from the map-series analysis revealed that the activation patterns were a lot more diffuse in the older observers (see Figure 28 vs. Figure 27 for the young subjects), which fits with the above-mentioned findings.

The activation of supplementary brain areas in older people could either be interpreted as an insufficiency to recruit the adequate neural networks (Logan et al. 2002), but also as a sign of compensatory plasticity (Reuter-Lorenz et al. 2000), possibly for compensating diffuse cell loss in the aging brain (for example Landi & Rossini 2010). This activation of supplementary cortical areas could furthermore be the reason for an increase in response times (in behavioural tasks), because of the additional time required for the processing in these areas. A reorganization of the neural networks could therefore allow the continued functioning of perceptual performance, however, at the cost of a slow-down of processing speed.

It will require further study to find out whether the perception of ICs is qualitatively impaired in older observers, or simply delayed (for example by pinpointing an electrophysiological equivalent for the perception of enhanced brightness). Nevertheless, our psychophysical experiments, in which the older participants hardly made errors, despite of probable

perceptual deficits, provide evidence that cognitive top-down mechanisms can compensate for certain deficits in visual processing.

5. Literature

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6. Abbreviations

EEG	electro-encephalography
EOG	electro-oculogram
ERG	electro-retinogram
ERP	event-related potential
fMRI	functional magnetic resonance imaging
GFP	global field power
IC	illusory contour
LCD	liquid crystal display
LGN	lateral geniculate nucleus
LSD	least significant difference
LOC	lateral occipital cortex
MEG	magneto-encephalography
NS	non-shape
PET	positron emission tomography
RC	real contour
RT	response time
SK	Scheinkontur
SPECT	single photon emission computed tomography
UFOV	useful field of view
VEP	visual evoked potential

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